Effect of high levels of macronutrients on the trace element nutrition of *Pinus radiata*

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DEDICATION

To my family,
Ren, Jan, Katya, Greta, Oma
and Steve.

Thank you
for your love, support and encouragement.

Abstract

A number of experiments, using both field trial and pot trial techniques, were undertaken to investigate the effect of N addition at high rates on the growth and nutrition of radiata pine. Two field trials were designed to investigate the effect of increasing rates of N addition on young radiata pine plantation (Taheke) growing in a fertile ex-pasture soil north east of Rotorua and the effect of increasing rates of N and B addition on young radiata pine growing in the nutritionally poorer soils of Ashley Forest in Canterbury. One pot trial in sand culture investigated the effect of N source on the growth of radiata pine seedlings while a further two pot trials investigated the effect of increasing N and B addition at two rates of P.

In 1989 urea was added at 0, 250 or 500 kg N ha^{-1} to enhance the mild stem deformities that had been observed in young radiata pine trees at the Taheke site. The soil had a high nutrient status, presumably because of its pastoral land-use history, a high potential to nitrify and the major form of inorganic N was nitrate. While the amount of radiata pine stem deformity did increase during the trial, this was not a result of the fertiliser addition. The measurements of tree height and diameter were also not significantly affected by N addition. Subsequent soil analysis indicated that the amount of native N in the top soil was already high, approximately 3.1 and 1.8t ha^{-1} in the 0 to 10 and 10 to 20cm depths respectively, and therefore the fertiliser additions did not represent a large input to the system and the addition of N did not significantly affect the amount of total N% or mineral N in the soil.

At Taheke, the increasing addition of N significantly increased the foliar concentrations of N in the short-term and significantly decreased the concentrations of P, Ca and Mg during the trial presumably as a result of dilution and/or translocation. There appeared to be a relationship between Cu and N, in the foliage, and the number of kinks in the upper stem of the radiata pine trees. As Cu:N ratios in the foliage increased, the number of kinks decreased.

The characteristics of the trial site at Ashley Forest contrasted to those at Taheke because the soils had a low nutrient status, had a very low potential to nitrify and the major form of inorganic N was ammonium. The B status of the soil was also marginal for radiata pine growth. The fertiliser treatments consisted of N, added as urea, at 0, 200 or 400kg N ha^{-1} by B, added as ulexite, at 0, 3.7 or 7.4 kg ha^{-1}. The foliage sampling technique followed the life of fascicles from just after initiation in November, 1989, to full extension in May, 1990. The results showed that the concentrations and of amounts per fascicle of N and B significantly increased in response to the addition of the respective fertilisers while P and Mg significantly declined with increasing N addition. Retranslocation occurred for both P and B particularly during times of low soil moisture. The amount of retranslocation was increased with increasing N addition while the increasing addition of B reduced the amount of B retranslocation.

The results indicated that without B addition the foliar concentrations of B were marginal (i.e. 8 to 12$\mu g\ g^{-1}$) and were further reduced by the addition of N. This also occurred for P where the foliar concentrations were low (i.e. <0.12%) and significantly declined with increasing N addition even though a basal dressing of 14kg of P ha^{-1} had been added.

The addition of N increased fascicle weights, compared to the control, particularly at 200kg N ha^{-1}, but had no significant effect on tree heights at 6 months or at 3 years after fertiliser addition. However, when twelve trees were biomassed 1 year after fertiliser addition at Ashley, the total

above-ground weight of trees that had received 7.4kg B ha^{-1} and/or 400kg N ha^{-1} was significantly greater then the control trees. The results from the biomass indicated that 3.2% of the added N and 0.5% of the added B was had been taken up into the above-ground portion of the tree. There was no evidence of residual fertiliser N in the soil, however the addition of B at 7.4kg ha^{-1} had significantly increased the non-specifically adsorbed and specifically adsorbed soil B fractions in the 0 to 10cm and 10 to 20cm depths. The weed components at Ashley, mainly gorse and broom, may have been important sinks for the added fertiliser.

A sand culture pot trial further investigated the effect of the inorganic N-source, either ammonium or nitrate, on the growth and nutrition of radiata pine seedlings. The results indicated that nitrate-N nutrition increased the uptake of cations, particularly Ca, Mg and Fe, while reducing the uptake of P. The roots of the nitrate-fed seedlings were darker in colour and were more numerously and finely branched than the ammonium-fed seedlings.

Two sand culture pot trials, one at 4μg P ml^{-1} and the other at 8μg P ml^{-1}, further investigated the interaction between the addition of ammonium (at rates of 14, 35 and 70μg N ml^{-1}) and B (at rates 0.01, 0.05 and 0.1 μg B ml^{-1}) on radiata pine seedlings. Increasing N addition increased: N uptake, shoot dry weights, the dilution of nutrient concentrations in the shoots, the translocation of nutrients to the shoots, the efficiency of nutrient uptake by the roots, the physiological use efficiency of nutrients and the seedling height difference. The root dry weights decreased with increasing N addition. As B:N ratios declined in the shoots, with increasing N addition, the amount of seedling height difference (a simple measure of stem deformity) increased. The correlation was significant. The increasing addition of B, in the sand culture pot trials, increased seedling B concentrations and B:N ratios and the amount of B in the roots.

Across the two ammonium by B pot trials, the higher addition of P affected radiata pine growth by increasing the amount of N in the shoots.

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Chapter 1

Introduction

Pinus radiata D. Don, commonly known as radiata pine, is a softwood producing tree. A native of California, where its natural distribution is restricted to an area of less than 7,000 hectares (Forde 1966), radiata pine has been very successful in temperate regions of the southern hemisphere. In New Zealand, radiata pine has been planted on a range of sites where the annual rainfall varies from 350 to 3000mm and the monthly mean temperatures extend from 2.8°C in June to 18.3°C in January (Jackson and Gifford 1974). However, radiata pine is generally confined to areas receiving greater than 600mm of annual rainfall (Boomsma and Hunter 1990).

A history of radiata pine in New Zealand, from the earliest known plantings in 1856, has been given by Sutton (1984).

Early on in New Zealand, during and after the large scale forestry plantings in the 1920's and 1930's, little consideration was given to the nutritional requirements of radiata pine which was considered to be a pioneer plant capable of sucessfully growing on infertile sites (Will 1985). These areas typically consisted of poor soils, soils with nutrient deficiencies for agricultural production, steep topographies, a bad location, soils degraded by farming activities or a combination of these characteristics. Because of the scale of planting, both in area and over time, radiata pine research has been aimed at several key areas - 1) the development of improved planting stock, 2) the use of silvicultural management techniques, including fertiliser inputs, pruning and thinning, to optimise tree growth and production, and 3) the development of radiata pine wood products that are marketable both in New Zealand and overseas. The emphasis and amount of this research has given radiata pine the status of being the number one commercial forestry tree in New Zealand.

Agroforestry is a world-wide approach to land-use that includes a huge range of different ecosystems. Agroforestry is a concept rather than a technology (Percival and Hawke 1985) and is an opportunity for the optimum use of space and time (New 1985). In New Zealand it is most often represented by an integrated farming and timber operation (Percival and Hawke 1985) described as a silvo-pastoral system (Grainger 1980). The silvo-pastoral system with pine and livestock is a flexible land use system which can be altered to fulfil multiple objectives (Anderson *et al.* 1988, **Plates 1a and 1b**).

The use of radiata pine in agroforestry has been encouraged because, with wide spacing on these typically fertile sites, it was considered that timber production per hectare would be high (similar to that of conventional plantations) with the prospect of saw or veneer logs being produced in a shorter rotation. For instance, Knowles (1972) estimated that radiata pine at very wide spacing could produce $21m^3\ ha^{-1}\ yr^{-1}$ of saw logs on a 20 year rotation compared to a 35 year rotation for conventional regimes. Birk (1990) found the mean basal area of 13 year-old radiata pine on an ex-pasture site to be $42.2m^2\ ha^{-1}$ compared to $31.8m^2\ ha^{-1}$ on an adjacent ex-native forest site in New South Wales.

In New Zealand the forest management regimes used in agroforestry vary widely with tree densities ranging from 100 to 350 stems per hectare (Percival and Hawke 1985). Arthur-Worsop (1985) using computer-modelling evaluated the economics of agroforestry at 100 stems per hectare on a 30 year rotation and showed that agroforestry was more economic than pastoral agriculture or forestry

alone given standard conditions of management and site and a discount rate of 10%. However, the profitability of agroforestry is sensitive to tree harvesting costs, transport costs, and the costs of lost agricultural production from the area (Stewart 1985).

Plate 1a

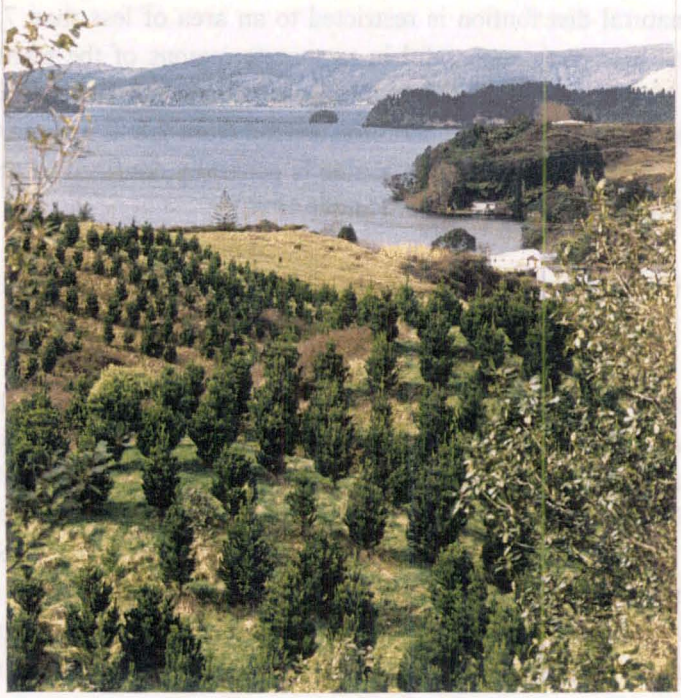

Plate 1b

Plate 1: Silvo-pastoral agroforestry with radiata pine at a) Taheke, a young radiata pine stand growing in an ex-pasture site overlooking Lake Rotoiti, north east of Rotorua, and owned by Tasman Forestry Limited and b) Tikitere, a maturing agroforest near Rotorua.

Thus, with high premiums being paid for good quality radiata pine saw logs and, more recently, the diversification in New Zealand's agricultural sector, a new era for radiata pine has developed - its introduction into the agricultural scene as a component of agroforestry.

The presence of forestry as an integral part of agriculture is seen to have many advantages than simply good economic returns. Morey (1988) found that the major reasons for farm tree planting (in order) were: stock shelter, house shelter, aesthetics, best land use, erosion control, own wood supply, increased farm value, and finally to make a profit from timber sales. However, in terms of land area and contribution to timber production it is the large owners (typically forest companies) that dominate the New Zealand agroforestry scene. Hammond (1988) reported that in the Rotorua Conservancy of the New Zealand Forest Service (which represented 38% of the national agroforestry area) 9283 hectares were grown by major owners and 757 hectares by small private growers. Hammond also found that the major forest owners concentrated more on radiata pine (used in 98% of agroforestry plantings) than the small owners (89%). According to Buckleigh (1988) the aim of major forest companies, such as Tasman Forestry Limited, was to produce clearwood in relatively short rotations with a trade-off between volume and quality per hectare resulting in increased value per hectare.

In the mid 1980's, it was observed that radiata pine, growing on the ex-improved pasture sites that were used for agroforestry establishment in both New Zealand and Australia, was exhibiting growth malformations. These defects which may appear during stem and branch development and are controlled by the site and/or genetic factors (Birk *et al.* 1989).

The research information currently available in New Zealand for radiata pine is largely based on trials conducted in conventional plantations. Recent investigations into radiata pine growth on ex-pasture soils suggest that there are fundamental differences between the agroforestry and conventional forestry systems. For instance, the history of radiata pine growth deformities in conventional forests has typically been related to specific nutrient deficiencies, such as copper (Cu) and boron (B), which have appeared on the poorer soils where many of these forests have been established. The answer to these problems has been the addition of a fertiliser containing the deficient nutrient. However, the specific causes for the growth deformities in agroforestry systems are unknown (Birk 1990) and/or the addition of a single fertiliser nutrient has typically not alleviated the problem (Carlyle *et al.* 1989, Hopmans 1990).

In agroforestry, the problem of radiata pine growth malformations has been practically solved by the selection of trees genetically capable of coping with the soil characteristics and resulting nutritional status. However, the theory behind the growth abnormalities needs to be identified as a step toward a better understanding of tree growth in these fertile soils which are markedly different from those previously investigated in conventional forestry systems.

1.1 GENERAL OBJECTIVES

The general objective of this PhD has been to gain a better understanding of nutrient interactions within radiata pine. The studies described have focused on N and its effect on the micronutrients Cu, zinc (Zn), and B in a variety of tree growing systems. The studies also attempted to identify relationships between growth deformities in radiata pine and the amount of nutrient in the soil-plant system.

Specific objectives accompany the research chapters 3 to 8.

1.2 RESEARCH OUTLINE

The motivation for this PhD study was the appearance in the 1980's of growth deformities in radiata pine grown on ex-pasture soils in agroforestry systems. During the PhD studies, the research emphasis moved toward a better understanding of nutrient interactions and how these may affect radiata pine tree growth.

The research programme began with a field trial in a 2 to 3 year old radiata pine agroforest known as 'Taheke', owned by Tasman Forestry Limited and situated north of Rotorua (Chapter 3). This site was an ex-pasture one with the trees exhibiting mild growth deformities. Here, increasing rates of N were added in an attempt to induce more serious growth deformities. Studies were also made of the soil profiles and the nitrification pathway at Taheke and other local sites including a pasture, adjacent to Taheke, and a mature plantation of radiata pine in Whakarewarewa Forest.

Further field work was carried out in Ashley Forest, a plantation forest in the Canterbury foothills now owned by Carter Holt Harvey Forests Limited. The soils at Ashley are nutritionally poor with a history of boron deficiency. Nitrogen and B fertilisers were added to investigate nutrient interactions in radiata pine foliage over a summer and autumn (Chapter 4). A biomass study was implemented one year after the Ashley trial began to identify the fate of the added fertilisers (Chapter 5).

A trace element fractionation scheme was used to identify the major forms of Cu, Zn and B in the soil profiles collected from Rotorua and during the Ashley biomass study (Chapter 6).

Finally, three pot trials were carried out to amplify the field trial work. Sand culture was used to grow radiata pine seedlings in a glasshouse environment with nutrients being added in solution. One trial investigated ammonium versus nitrate as the N source for seedling growth (Chapter 7) while the other two trials studied N and B interactions at two levels of phosphorus (P) and are described in Chapter 8.

Chapter 2

General literature review

2.1 RADIATA PINE FOREST SYSTEMS

2.1.1 Plantation forests

The 'plantation' forests in New Zealand, described as 'industrial forestry' by Sutton (1984), are the traditional planting of radiata pine. They consist of large areas of monocultures of radiata pine planted on soils originally considered unsuitable for agriculture and grown specifically for the production of timber.

Much forest research in New Zealand has focused on the nutrition of radiata pine and how certain fertilisers may improve tree growth and productivity in plantation forest systems, by alleviating the various nutrient deficiencies associated with the different soils that radiata pine has been historically planted on.

2.1.2 Ex-pasture sites

The characteristics of radiata pine agroforests in New Zealand have been described in Chapter 1.

In both New Zealand and Australia, forestry on ex-pasture sites has become an important radiata pine land-use option because of the potential for high growth rates on these fertile sites. While ex-pasture plantations generally have a greater total productivity than similar ex-forest sites, the merchantable volume may not be as great (Turner and Lambert 1991). This is because of the development of growth deformities and general poor form of radiata pine trees on these sites. According to Birk *et al.* (1991), there is a lower recovery of sawn timber from ex-pasture trees and the overall value per tree is about 30% less than the value of comparable ex-native forest trees.

2.2 GROWTH DEFORMITIES OF RADIATA PINE

Within plantation forest systems, radiata pine growth deformities have tended to be the result of a specific nutrient deficiency. Other than N, P, and B the only other nutrients identified in exotic plantations as being deficient are Cu and potassium (K) in New Zealand (Ballard 1978). Further nutrients have been added to the list including magnesium (Mg) (Will 1985, Payn 1991), calcium (Ca) (Will 1985), sulphur (S) (Turner and Lambert 1978) and Zn (Boardman and McGuire 1990a, Thorn and Robertson 1987). Those nutrients that are routinely applied as fertilisers to deficient areas in New Zealand are N, P and B (Will 1985) with other fertilisers being applied as nutrient deficiencies are identified. A description of nutrient deficiency symptoms in radiata pine plantations is given by Will (1985).

There are plantation forests grown on high nutrient status soils. For instance, Lambert and Turner (1977) describe the growth deformities associated with 'high site quality' dieback in New South Wales, Australia, and some areas of Tarawera and Kaingaroa Forests in New Zealand. However, the most recent cases of radiata pine growth deformities have been identified in agroforestry and ex-

pasture systems, particularly where the planting sites have been previously used for pasture or crop production. These growth deformities have been described as the 'speed wobbles' syndrome (Will 1986, Shoemark 1988, Will 1990) and the 'Toorour' syndrome (Carlyle *et al.* 1989, Downes and Turvey 1990, Turvey and Grant 1990). It appears that both these syndromes are describing very similar, if not the same, growth deformities of radiata pine.

Boomsma and Hunter (1990) noted that malformations such as the Toorour and speed wobbles syndromes on ex-improved pastures were considered to be widespread.

2.2.1 Visual symptoms of the ex-pasture growth deformities of radiata pine

The Toorour syndrome has been used in Australia to describe the situation where visual symptoms similar to Cu deficiency were seen but Cu levels in the foliage appeared adequate and the trees did not respond to the addition of Cu fertilisers (Turvey and Grant 1990). The foliar concentrations of Cu were also consistently above those levels at which Cu deficiency symptoms appear (Carlyle *et al.* 1989). In New Zealand the term 'speed wobbles' has been used to describe the rapid growth of radiata pine that is accompanied by distorted growth seen as stem and branch twisting (Will 1986).

In the literature, photographs of these deformities generally show radiata pine trees that differ greatly from the most desirable form which, according to Birk *et al.* (1989), is one that is 'vigorous, straight, single stem with slight branches that leave minimal knot formation following pruning'. On ex-pasture sites the poor form of radiata has been due to three major problems: bent and twisted stems (sinuosity), lack of apical dominance and heavy branching (Birk 1990).

Plate 2a **Plate 2b**

Plate 2: Examples of a) mild and b) more severe radiata pine stem deformities at Taheke, north east of Rotorua.

The visual evidence of speed wobbles seen in New Zealand **(Plates 2a and 2b)** is mild compared to the spiralling centre leader in Shoemark (1988), Bail and Pederick (1989) and Hopmans (1990), the severe stem deformities in Carlyle *et al.* (1989) and the 360° loop in Hopmans (1990). However, mild twisting and kinking of the new centre leader of radiata pine is a relatively common sight in shelter belts, agroforests and ex-pasture systems throughout New Zealand.

The radiata pine stem malformations that have occurred can be placed in the following categories 1) malformations caused by mechanical effects, 2) malformations caused by a specific nutrient deficiency and which can be cured by the addition of the nutrient, and 3) malformations that may resemble a particular nutrient deficiency where the addition of that nutrient does not alleviate the symptoms. Both the Toorour and speed wobbles syndromes can be placed in category three - the symptoms resemble Cu deficiency but the addition of Cu fertiliser does not prevent the development of the malformations.

2.2.2 Factors associated with radiata pine growth deformities in ex-pasture systems

To date, evidence points to several factors, including genetics, nutrition, soil chemical properties and climate, involved in the poor form of radiata pine on ex-pasture sites (Birk 1990, Will 1986).

2.2.2.1 Site and soils

Carlyle *et al.* (1989) concluded that the Toorour growth syndrome of radiata pine were associated with land-use history rather than soil type or lithology. Radiata pine growth deformities are typically found on ex-pasture soils (Will 1986, Hunter *et al.* 1990a) which have a high fertility (Shoemark 1988). The most severe growth deformities have been found on cleared legume-improved sites (Birk *et al.* 1991).

It appears that the presence of high levels of nitrate in the soil and/or the potential of the soil to nitrify at high levels has been the common finding of ex-pasture soils where the stem deformities have occurred (Shoemark 1988, Carlyle *et al.* 1989).

Other soil factors that may be associated with the growth deformities include low pH and high exchangeable aluminium (Al) (Birk 1990), a high availability of manganese (Mn) (Shoemark 1988, Carlyle *et al.* 1989) and high soil P (Shoemark 1988).

2.2.2.2 Nutrition

When stem deformities were first encountered in radiata pine ex-pasture systems, researchers (e.g. Pederick *et al.* 1984, Will 1985, Turvey and Grant 1990) suspected Cu was involved as the deformities were similar to those symptoms exhibited by Cu deficient trees. However, as the addition of Cu fertilisers did not alleviate the visual symptoms other hypotheses have been formulated to explain the presence of growth deformities. Examples are: high nitrate-N production or relative nitrification in the soil (Carlyle *et al.* 1989, Hopmans and Flinn 1991), the addition of high rates of N fertilisers Hopmans and Flinn 1991), higher levels of foliar N and P with possible cation imbalances (Turner and Lambert 1991), high levels of available Mn (Carlyle *et al.* 1989, Turner and Lambert 1991), high levels of Al (Turner and Lambert 1991), imbalances between N and other nutrients such as B, S, and P (Birk *et al.* 1991), and limiting micronutrients (Turner and Lambert 1991).

Carlyle *et al.* (1989) concluded that the growth syndrome was unlikely to be a result of a single micronutrient deficiency or other element deficiencies.

2.2.2.3 Genetics

In Victoria, Australia, speed wobbles was first observed in 1981 in a genetics trial of radiata pine families where the families varied in the degree of deformity displayed (Shoemark 1988). Pederick *et al.* (1984) concluded that the more severe growth malformations could be explained in terms of an individual genetic affect.

There is a range of examples in the literature that has shown what effect clone or family has on foliar nutrient concentrations (e.g. Lambert and Turner 1977, Knight 1978, Pederick *et al.* 1984). Graham (1981) described the ways in which genotypic differences could affect the plant absorption of Cu: 1) differences in the rate of absorption of Cu by the roots, 2) better exploitation of soil through greater root length, 3) better contact with the soil via long root hairs, 4) modification of availability of Cu in soil adjacent to roots by root exudation, 5) acidification or change in redox potential, 6) more efficient retranslocation of Cu from old tissues to the growing points, 7) lower tissue requirement for Cu, and 8) high rates of Cu absorption. These factors could all be involved in making a particular genotype better adjusted to growth on a soil of low Cu availability. It is likely that these factors would also affect the absorption of other soil nutrients.

In Australia, the genetic selection of radiata pine that will produce a stem of straight form on ex-pastures has solved the practical problem of stem deformities on high fertility soils (e.g. Bail and Pederick 1989). The gains from genetic tree improvement are two-fold: 1) gains in volume growth rate which results in a greater wood volume or as reduction in rotation length of 2-3 years (Shelbourne *et al.* 1989), and 2) improvement of tree form traits which may result in a 50 to 80% increase in the frequency of "acceptable trees for final crop" (Wilcox and Carson 1990). However there still remains the question of why these stem deformities were occurring and how nutrient interactions in the growing system affect radiata pine growth.

2.2.2.4 Climate

Important physiological processes are often inhibited by environmental stresses like drought, nutrient deficiencies, unfavourable temperatures and air pollution (Kramer 1986). Will (1986) suggested that speed wobbles was caused by environmental stresses (e.g. wind and rain) that occurred while radiata pine was growing rapidly and in a susceptible state (i.e. rapidly elongating soft shoots).

2.3 NITROGEN, COPPER, BORON AND ZINC NUTRITION OF RADIATA PINE

The evidence to date suggests that the high levels of soil N in ex-pasture sites may have been causing imbalances between N and other nutrients within radiata pine. This situation contrasts with the presence of marginal N deficiencies in plantation forests of radiata pine throughout New Zealand (Will 1985).

Micronutrients are not generally added to soils during the management of pastures so that, depending on the soil parent material, the amounts of micronutrients may be low compared to the amounts of macronutrients present. Hill and Lambert (1981) noted that of the micronutrient deficiencies

reported in New Zealand and Australia, Cu, Zn and B were the most widely reported for radiata pine. Generally micronutrient problems appear in young forest stands within a few years of planting and essentially involve insufficient micronutrient uptake from the soil (J.A. Adams and R.G. McLaren, unpublished).

2.3.1 Nitrogen

Within the plant nitrogen is essential to many functions. Nitrogen is viewed as a nutrient that is central to the growth of plants because of its role in substances such as proteins, chlorophyll, nucleic acids, and nucleotides and nucleosides (Haynes 1986a).

Within radiata pine, satisfactory foliage standard values for N range from 1.2 to 1.5%.

2.3.2 Copper

Copper is involved in many basic physiological reactions involving the synthesis of metabolites, physiological steps in development, and differentiation as well as in catabolism and turnover (Bussler 1981). Cu protein forms are widely distributed and perform major metabolic functions in the plant so that associated behaviour of N and Cu in many plant species seems a fundamental factor in the behaviour of Cu in the biology of plants (Walker and Webb 1981). Copper is important in the cell wall metabolism and has its most important effect in the latter stages of stabilisation - during lignification (Bussler 1981). Copper is not readily mobile within the plant but it may be translocated from older to younger leaves (Mengel and Kirkby 1987).

A Cu deficiency in radiata pine produces the following visual symptoms: the twisting of branches and a flatter branch angle, twisting of the leader, a higher incidence of needle fusion, and needle tip burn (Will 1971). In radiata pine plantations, the critical concentration range for Cu in the foliage is 2 to 4$\mu g\ g^{-1}$ (Will 1985).

While a Cu deficiency may appear to be the syndrome most common in malformed trees, both the soil environment and the tree may also contain complex deficiencies and excesses of elements which could exacerbate the manifestation of the syndrome, and make correction of the apparent deficiency much more difficult (Turvey and Grant 1990). Other factors that cause similar symptoms include branch twisting due to K and B deficiencies reported in Australia, wind (especially strong and from one direction) and rain, and some herbicides which can cause a single twisting event rather than the twisting over successive years as occurs with Cu deficiency (Will 1985).

2.3.3 Boron

The biochemical role of B in the plant, according to Gupta *et al.* (1985), is not yet well understood. According to Wells (1968), B is involved in many plant processes including flowering, fruiting, germination by pollen, cell division, N metabolism, carbohydrate metabolism, salt absorption, hormone movement and water relationships. The hypothesis that B is involved in the formation of the cell wall is based on the well-known ability of B to produce complexes with sugars and pectin substances (Shkolnik 1984). Both Ca and B have been implicated in the lignification process (Wardrop 1981).

Boron is readily translocated through the xylem translocation stream (Gupta *et al.* 1985) but was thought to be immobile once it reaches the foliage - it may move within the leaf but cannot be withdrawn (Stone 1990). However, recent evidence suggests that B can be retranslocated from needles (Hopmans and Clerehan 1991).

Boron deficiency is the most commonly-seen micronutrient problem in New Zealand exotic forests and occurs over a range of soil groups (Adams *et al.* 1991). In young radiata pine, the first visible symptoms of B deficiency are wavy branches and main stems, resin bleeding, and the tip death of the leader or major branches (C.J. Borough, W.J.B. Crane and C. Johnston, unpublished). According to Lambert and Turner (1977) severe B deficiency in *Pinus* species results in the repeated dieback of the apical meristem, a failure to develop mature needles and the roots are reduced in size and number. Marginal B deficiency leads to relatively normal tree growth but with occasional leader dieback (Lambert and Turner 1977). A relatively common feature of young trees on ex-pasture sites is a bushy form with tip die-back associated with B deficiency (Birk *et al.* 1989, Birk 1990).

Severe deficiency of B is generally associated with levels of 8μg g^{-1} or less in radiata pine foliage, with marginal deficiencies in the 8 to 12μg g^{-1} range (Lambert and Turner 1977). These critical levels are also used in New Zealand but, according to Will (1985), some stands have been unaffected in spite of levels as low as 6μg g^{-1}. Boron concentrations in the foliage are considered satisfactory if they are greater than 12μg g^{-1} (Will 1985).

In assessing the possible development of B deficiency, other factors such as climate and soil moisture have to be also considered (Will 1985). Limited supplies of B or even a brief interruption in its absorption can cause irreversible damage to rapidly growing shoots (Stone 1990).

2.3.4 Zinc

Zinc is particularly important in forestry for its essential role in gene replication and its regulation of tryptophan synthesis as a precursor of auxin - the first ensures the replication of the species and new growth in expanding cell numbers while the latter ensures that this growth can proceed (Boardman and McGuire 1990b).

In radiata pine, visual symptoms of Zn deficiency include stunted growth in young trees and a rosette of buds at the terminal which, in Australian experience, can result in severe malformation due to multileaders (Will 1985) as a result of shoot tip dieback (Boardman and McGuire 1990a).

Most radiata pine forests in New Zealand have foliar Zn concentrations of 30 to 50μg g^{-1} (Will 1985) while the deficiency range is 5 to 12μg g^{-1} (Hill and Lambert 1981).

2.4 SOIL NITROGEN, COPPER, BORON AND ZINC

Much of the literature regarding radiata pine growth on ex-pasture sites is Australian. As noted by Turner and Lambert (1991), the nutrient status of the soil is greatly affected by the soil parent material it was formed from. The major parent materials, described as the 'rock class', on which soils have developed and have been subsequently planted in forestry in Australia are argillaceous (e.g. shale, slate, siltstone, mudstone, pelitic tuff, greywacke and clay mantles), ferromagnesian (e.g. spillite, basalt, dolerite, andesite, gabbro, and greenstone), shallow sands, medium to coarse grained

feldspathic-quartzose (e.g. grandiorite, quartz dirite, monzonite, and diorite) and deep sands (Turner and Lambert 1991, Turner *et al* 1990). These parent materials represented 35, 16, 16, 15 and 11% respectively of the 993,965ha of total afforested area in Australia, in 1990, of which 669,700ha was radiata pine (Turner and Lambert 1991). Because of the range of soil parent materials on which forestry plantations grow in Australia, there is a corresponding range of soil nutrient levels and chemical characteristics in the surface soils. For instance, Turner and Lambert (1991) cite the following ranges: total soil P from 42 to 1495μg g^{-1}, N from 0.03 to 0.46%, and pH from 4.7 to 5.9. A number of nutrient deficiencies, including N, P, K, Ca, Mg, S, Cu, Zn, B and Fe, have been associated with radiata pine growth on different soil parent materials in Australia (Turner and Lambert 1986). Since 1970, there has been change in the land base of radiata pine forestry toward the higher nutrient soil parent materials, including ex-pasture sites, which suggests that the planes of nutrition will be considerably different (Turner and Lambert 1991).

In New Zealand, there are also a wide range of soil parent materials which contribute to the soils on which radiata pine plantations are grown. These include a variety of volcanic parent materials in the North Island (Madgwick *et al.* 1977, Hunter and Graham 1982, Hunter *et al.* 1985), glacial outwash gravels (Adams 1973), greywacke gravels with thin loess deposits (Mead *et al.* 1984), coastal sand dunes (Gadgil *et al.* 1984) and others.

2.4.1 Nitrogen in the soil

Ammonium (NH_4^+) is the major form of nitrogen available for tree uptake in plantation forest systems while in the agricultural system nitrate (NO_3^-) is the major form of nitrogen available. The different forms of N present in these two systems are related to the nature of the soil which dictates the kind of soil microorganisms controlling the nitrification pathway. Soil factors which can influence the type of nitrifying microbial populations present include soil characteristics such as pH (Focht and Verstraete 1977) and the influence of plants on the soil through the C:N ratio of the litter (Haynes 1986b) and the excretion of componds by the plant roots that may be deleterious to the microbes (Alexander 1977).

The nitrification pathway is discussed in more detail in Chapter 3. The source of N, either as ammonium or nitrate, affects other aspects of nutrient uptake which is discussed in detail in Chapter 7.

Both the amount and form of nitrogen and how it affects other nutrients - in the soil, during the uptake process and within the plant itself - appears to be an important but, as yet, poorly understood component of tree nutrition in the ex-pasture system.

2.4.2 Copper, boron and zinc in the soil

Within the soil, micronutrients are found in the soil solution, adsorbed at the surfaces of soil colloids, occluded by soil oxide materials, present in the structures of secondary minerals and other inorganic compounds or present in the structures of the primary minerals (McLaren and Cameron 1990).

2.4.2.1 Total levels

According to Knezek and Ellis (1980), the igneous rocks, granite and basalt, contained an average of 10 and 100μg g^{-1} Cu respectively while the sedimentary rocks of limestone, sandstone and shale contained an average of 4, 30 and 45μg g^{-1} Cu respectively. The Zn content of soils can range between 10 and 300μg g^{-1} (Knezek and Ellis 1980) but is generally between 30 and 100μg g^{-1} (Boardman and McGuire 1990b). Total B in the soil, which depends on the parent material and the degree of weathering, ranges from 1 to 270μg g^{-1} with an average of 20 to 50μg g^{-1} (Barber 1984).

2.4.2.2 Soil solution

The concentrations of micronutrients in the soil solution can vary substantially depending on the soil parent material, the chemical and biological processes within the soil and the measurement technique used. Kabata-Pendias and Pendias (1984) found that the concentrations of Cu, Zn and B in the soil solution ranged from 0.0005 to 0.14, 0.001 to 17 and 0.07 to 3μg ml^{-1} respectively.

The plant uptake of these micronutrients is generally in ionic forms from the soil solution (J.A. Adams and R.G. McLaren, unpublished). Common forms of Cu, Zn and B in the soil solution are Cu^{2+}, Zn^{2+} and H_3BO_3 respectively (Bohn *et al.* 1985). At higher soil pH values, other forms of Cu, Zn and B may also exist in solution such as $B(OH_4)^-$ (Sposito 1989), $CuOH^+$ (Knezek and Ellis 1980) and $ZnOH^+$ (McLaren and Cameron 1990) respectively.

The capacity of the soil to maintain adequate concentrations of micronutrients in the soil solution is a major factor affecting the plant availability of micronutrients from the soil (J.A. Adams and R.G. McLaren, unpublished). The solution concentrations of B, Cu and Zn are probably governed by adsorption/ desorption reactions at the surface of the soil colloids (J.A. Adams and R.G. McLaren, unpublished, McLaren *et al.* 1990).

The release of organic compounds by microbes and plant roots into the rhizosphere can complex Zn and Cu and could enhance the solution concentrations of these nutrients and increase their rate of transport to the plant roots (J.A. Adams and R.G. McLaren, unpublished). Organic complexing can account for a large proportion of Cu (Turvey and Grant 1990) and Zn (Jenkins and Wyn Jones 1980) in the soil solution.

2.4.2.3 Soil adsorption processes

For Cu^{2+} and Zn^{2+}, the normal cation exchange mechanisms are not considered to be of major importance because of the much higher levels of the major nutrient cations (e.g. Ca^{2+}, Mg^{2+} and K^+) which, by a mass action effect, tend to exclude any significant amounts of micronutrients from the cation exchange sites (J.A. Adams and R.G. McLaren, unpublished).

Adsorption equilibria govern the ionic concentrations of elements such as Co, Zn, Mo, Cu and B (Quirk and Posner 1975). The soil adsorption of B, Cu and Zn is thought to be specific. This refers to the formation of stable complexes between the micronutrient ion/compound and certain functional groups at the surface of inorganic colloids, principally oxides and hydrous oxides of iron (Fe), Al and Mn and also on variable charge edge sites of aluminosilicate clay minerals, or soil organic colloids (J.A. Adams and R.G. McLaren, unpublished).

The association of Cu with the mineral colloids of Al, Fe, and Mn limits the mobility of Cu and its availability to plants (Jarvis 1981). Copper is bound more strongly to the organic matter than are other micronutrient cations, such as Mn and Zn, and the complexes of organic Cu are important in regulating Cu mobility and availability in the soil (Mengel and Kirkby 1987). The percentage of soil copper associated with organic matter would be high in organic rich soils and influenced by soil properties as pH and the type and amount of clay (Stevenson and Fitch 1981). Much of copper's soil chemistry, according to Knezek and Ellis (1980), is related to S and organic matter due to its strong covalent bonding.

Boron sorption studies, according to Evans and Sparks (1983) have suggested several mechanisms between B and the soil including 1) sorption of borate ions, 2) sorption of molecular boric acid, 3) formation of organic complexes, 4) precipitation of insoluble borates with Al and Si, and 5) B entry into clay structures. Jin *et al.* (1988) found that clay and Al, Fe and Mn oxyhydroxides had an affinity to absorb a portion of applied water soluble B in relatively unavailable forms. The process of desorption releases B from the solid phase and largely controls the amount and release of both native and fertiliser B for uptake by plants (J.A. Adams, Z. Hamzah and R.S. Swift, unpublished). Boron in soil organic matter is mainly in the surface soil horizons (Gupta *et al.* 1985) and can account for much of the soil's total B which is made available to plants by microbial activity (Evans and Sparks 1983). Under droughty conditions microbial activity declines and the B therefore remains complexed with the organic matter and unavailable for plant uptake (Berger 1962).

Barber (1984) stated that adsorption of Zn by soils increases with increasing CEC, clay content, organic matter levels, pH and the presence of $CaCO_3$. Zinc can be in coordination complexes with soil organic matter and may be replaced by Cu which has a higher stability constant (Barber 1984).

2.4.2.4 Soil oxide materials

Micronutrients become occluded in the developing coatings and concretions of oxides and hydrous oxides of Fe, Al and Mn in soils (McLaren and Cameron 1990). Both Fe and Mn oxides have a high sorption capacity for micronutrients and large amounts can be accumulated in nodules and Fe- and Mn-rich points (Kabata-Pendias and Pendias 1984).

2.4.2.5 Mineral structures

A large proportion of micronutrients in most soils will remain in the structure of secondary and, where present, primary minerals (J.A. Adams and R.G. McLaren, unpublished).

2.5 FACTORS INFLUENCING MICRONUTRIENT AVAILABILITY

The ecosystem consisting of forestry in an ex-pasture is one of dynamic and complex nutrient flows. According to Hill and Lambert (1981) the factors influencing micronutrient uptake are the processes of uptake, root distribution, micronutrient interactions, environmental effects, and tree genotypes. Thus studying micronutrient nutrition should involve the whole ecosystem which influences tree growth as well as the relevant tree characteristics.

2.5.1 Soil chemical and physical properties

Within the soil there is a range of features - both chemical and physical - that can affect the plant availability of micronutrients. According to J.A. Adams and R.G. McLaren (unpublished) micronutrient availability is strongly related to the soil properties such as organic matter, pH and texture. The adsorption of B, Cu and Zn is known to increase with increasing of soil pH and increasing levels of organic matter (J.A. Adams and R.G. McLaren, unpublished). Copper availability in the soil is also controlled by metal oxides (Turvey and Grant 1990) particularly iron (Fe) and Mn oxides (Kabata-Pendias and Pendias 1984).

As with agricultural crops, Cu deficiency in conifers has been found in trees grown in sandy soils low in Cu, and in soils such as peats, podsolised sands, and calcareous soils, which are capable of binding Cu (Turvey 1984) and very acid soils (Hill *et al.* 1981). In all these soils the deficiency may be exacerbated by poor drainage (Turvey 1984) and salinity (Raupach *et al.* 1978).

The potential plant uptake of micronutrients can be reduced by antagonistic or competitive elements within the soil. Many elemental interactions can be explained in terms of competition between chemically similar elements for a common metabolic pathway e.g. Zn can induce Cu deficiency (Boardman and McGuire 1990b) and the plant absorption of Zn can be inhibited by Ba, Sr, Ca and particularly Mg (Chaudhry and Loneragan 1972). While much circumstantial evidence for interactions of Cu with Mn, Zn, and Fe in particular exists (Turvey and Grant 1990), none of these elements are in isolation in the soil and it is likely that each element has an important effect on the uptake of other elements by trees.

The behaviour of Cu, Zn, Mn, and Fe appears to be most antagonistic or synergistic in acid soils and in association with increased N supply, especially as nitrate (Turvey and Grant 1990). Because of these interactions, deficiencies or toxicities of particular elements in plants cannot be investigated separately.

2.5.2 The addition of macronutrients to the soil

The addition of macronutrients to the soil can influence the availability of micronutrients. Of the macronutrients added to soils the most common in New Zealand pastoral history would be P, S and Ca from superphosphate, and N from both fertiliser additions and the symbiotic fixation of N in legumes. Hill and Lambert (1981) state that the interactions between micronutrients and macronutrients fall into two main categories - relationships found between nutrients in the plant and where a treatment is applied, such as N fertiliser, and another nutrient, such as Cu or B, is affected.

Urea was the fertiliser used as a source of N in the field trials described in this thesis. Urea [$CO(NH_2)_2$] is a highly soluble form of N which can move freely in soil water (During 1984) and has the highest N concentration (46%) of any solid fertiliser commonly used (McLaren and Cameron 1990). After addition to the soil it is converted to ammonium (soil pH rises) with the possibility of ammonia volatilisation. However in the long term, fertilisers containing NH_4^+ ions or urea will cause soil acidification whether the ions are directly taken up by plants or nitrified first (Rowell and Wild 1985). This is due to the conversion of NH_4^+ to NO_3^- which is susceptible to leaching and, along with it, basic cations such as Ca^{2+} are also leached (McLaren and Cameron 1990).

Cu deficiency can be induced, or accentuated, in plants grown in susceptible soils by the application of N and P fertilisers (Turvey 1984, Turvey and Grant 1990, Will 1985), high levels of N in the soil (Hill *et al.* 1981) and by the increase in soil N content by legumes (Will 1971). Pederick *et al.* (1984) found that the relationship between Cu and N levels was not significant but the foliar concentration of Cu was directly related to P levels which were particularly high and typical of those from trees growing on ex-agricultural soils which had received phosphorus fertiliser. According to Jarvis (1981) an increased supply of P from soil may restrict Cu transport from roots to shoots.

Among the factors reported by Boardman and McGuire (1990b) that may induce Zn deficiency are high soil available P levels, high N fertiliser applications, and high levels of mineralisable soil N in improved pastures. McGrath and Robson (1984) studied the effect of N and P supply on the response of radiata pine seedlings to the application of Zn. They found that the occurrence of zinc deficiency, after transplanting and the application of N and P, was largely due to a dilution of Zn within the seedlings rather than a restriction of absorption or utilisation of Zn by P or N.

Clear manifestations of B deficiency and/or a reduced B foliar level may be induced by the addition of macronutrient fertilisers (Stone 1990). Pasture improvement, according to C.J. Borough, W.J.B. Crane and C. Johnston (unpublished) often results in soil acidification and the use of lime as a treatment to overcome this could enhance B deficiency problems. Both Ca and Mg, nutrients found in lime, affect the plant uptake of B (Snowdon 1982, Gupta *et al.* 1985).

2.5.3 Climate

One of the reasons radiata pine is selected for forestry plantings is its ability to be highly productive over diverse climatic conditions (Turner and Lambert 1986). In New Zealand, radiata pine grows on a wide range of sites where annual rainfall varies from 350 to 3000mm, and monthly mean temperatures from 2.8°C in June to 18.3°C in January (Jackson and Gifford 1974). As previously mentioned, much of the literature regarding radiata pine growth on ex-pasture sites is Australian. In Australia, radiata pine is grown in coastal and tableland areas where annual rainfall ranges from 700 to 1500mm and includes summer, uniform and winter-dominated rainfall patterns (Turner and Lambert 1986).

According to Boomsma and Hunter (1990), the amount and distribution of annual rainfall is used to highlight climatic differences between Australia and New Zealand. Because almost half of the radiata pine plantations in Australia recieve less than 900mm of annual rainfall (Booth and McMurtrie 1988) while plantations in the North Island of New Zealand recieve an annual rainfall of 870 to 2300mm, with an average of 1450mm (Hunter and Gibson 1984), Australian research has tended to concentrate on the conservation of limited soil moisture and improving the efficiency of water use, whereas research in New Zealand has focussed on the improvement of growth under conditions of excess moisture (Boomsma and Hunter 1990).

An important feature of climate is rainfall. Although the absolute rainfall amount is important, its yearly distribution in conjunction with temperature and soil moisture storage controls radiata pine growth patterns (Boomsma and Hunter 1990). Water is a critical factor which directly influences the supply of nutrients from the soil to the growing tree (Turner and Lambert 1991) especially those nutrients, such as B, taken up by mass flow (J.A. Adams, Z. Hamzah, and R.S. Swift, unpublished) and diffusion. The amount of water a soil can hold depends on soil physical properties, organic matter levels, soil depth, and the presence of layers which may impede drainage (Gholz *et al.* 1990).

Boomsma and Hunter (1990) list several management practices that enhance moisture relationships. Water availability must be considered in relation to the plantation species physiological and morphological characteristics (Turner and Lambert 1991).

Climatic stresses (such as low rainfall) in marginally deficient sites have induced or enhanced the symptoms of micronutrient deficiencies in *Pinus* species (Hill and Lambert 1981). Of the three micronutrients under study, certainly B appears to be most affected by climatic conditions - particularly rainfall. The onset and severity of B deficiency symptoms (dieback of buds and shoots) in radiata pine are closely related to moisture stress (Will 1985). In Canterbury, soils with an actual or marginal B deficiency include Dystric and Eutric Cambisols in areas of low rainfall (Adams *et al.* 1991). In the North Island low levels of foliage B occur on some coarse pumice soils and dieback symptoms have been reported especially in dry years (Will 1985).

Continuing research into practices which conserve soil moisture for plantation use (Boomsma and Hunter 1990) appear to be fundamental for the improvement of radiata pine growth particularly in drier areas.

Temperature also influences micronutrient uptake - directly, by affecting chemical reactions within the soil, and indirectly, by affecting the root system. Temperature affects B uptake per root weight and partly by affecting root system size can have a profound effect on B uptake (Gupta *et al.* 1985).

2.5.4 The competing ground cover

In plantation forestry, there are a variety of 'weeds' such as gorse, blackberry, bracken, broom, regeneration of other tree species, and grasses which compete with the trees for resources such as soil water and nutrients. In agroforestry and ex-pasture systems in New Zealand the pasture sward represents the major vegetative competition to trees. Buck (1986) described the sharing of the resource pools in agroforestry as competitive, differential and complementary.

The availability of water and nutrients are affected by competing vegetation (Turner and Lambert 1986). Nambiar and Zed (1980) discussed the effect of weeds in plots of young radiata pine and concluded that the effect of weeds on the uptake of nutrients by the young trees was largely due to the soil drying rather than the direct competition for nutrients. They suggested that on relatively dry sites even a 5 to 10% surface weed cover could induce a level of water stress (-1500 to -1800 kPa) that would impair growth.

Boomsma and Hunter (1990) noted that former agricultural land was increasingly being used for plantation forestry and that the past two decades had produced a 'growing sophistication' in the management of weed competition.

2.5.5 The tree root system

Water and nutrient uptake are greatly influenced by root development (Turner and Lambert 1991). The distribution, frequency of root size and root depth are critical factors in nutrient acquisition (Hill and Lambert 1981) particularly where root interception with nutrients, such as Cu and Zn, is important. Nambiar (1983) found that the root densities of young radiata pine growing on sandy soils were among the lowest reported for plants at 0.05 to 0.32cm cm^{-3}. Squire *et al.* (1978) found

root densities of a developed radiata pine stand (8 years old) to be 0.8 to 2.2cm cm^{-3}. These values are considerably lower than the density of 30 to 50cm cm^{-3} for pasture roots in the top 10 cm of the soil reported by Barley (1970).

Root development may be limited by soil physical characteristics such as a high bulk density (Turner and Lambert 1991). Nambiar *et al.* (1984) considered the management of roots and genetic selection to enhance the efficient use of soil resources. Such resources would include micronutrients.

2.5.6 The rhizosphere

The rhizosphere describes the 1 to 2mm zone surrounding the surface of the root (Ross 1989) and is affected by many factors including the kind and stage of development of the trees, the soil's physical and chemical properties and moisture content, other environmental conditions such as light and temperature (Pritchett and Fisher 1987), the root's response to the plant nutritional status and soil microorganisms (Marschner *et al.* 1987).

Both the pH and the microbial activity of the rhizosphere can be different from that in the bulk soil (McLaren and Cameron 1990). The pH of the rhizosphere may be more acidic than the bulk soil if the plant is absorbing more cations than anions (Sposito 1989) and higher microbial populations exist in the rhizosphere possibly due to the presence of organic exudates and debris from the roots (Barber 1984). Both of these factors can affect the availability of nutrients to roots.

2.5.7 Mycorrhiza

The host tree can derive several benefits from mycorrhizal associations: 1) increased nutrient uptake, 2) increased water uptake and drought resistance, 3) resistance to certain root pathogens, and 4) increased tolerance to toxins, temperature extremes and adverse pH levels (Jackson and Mason 1984). Such benefits from the symbiotic association between trees and the mycorrhizal fungi usually far outweigh the energy cost of the fungus (Bowen 1980).

Mycorrhizal associations with radiata pine have been found to increase Zn uptake (Bowen *et al.* 1974), increase soil exploitation and the amount of nutrients, especially P, available for uptake (Attiwill and Leeper 1987), and readily utilise ammonium N (Bowen and Smith 1981).

Studies by Chu-Chou and Grace (1987) have found that a change of mycorrhizal fungi occurs in radiata pine trees planted on ex-pasture sites - from the common and efficient *Rhizopogon rubescens* found in plantation forests to the less common and less efficient *Tuber* sp. and *Scleroderma* sp. and questioned the necessity and benefit of mycorrhizal fungi for radiata pine at these sites.

It appears that high levels of macronutrients may affect mycorrhizal development. For instance, Timmer and Leyden (1980) found a decrease in plant Cu contents at high P due to a reduced exploitation of soil by mycorrhiza which led to a decrease in Cu absorption.

2.5.8 Soil organisms

Soil organisms, from microflora and microfauna to macrofauna, are involved in many soil processes including the formation and development of the soil, nutrient cycling, litter decomposition, the metabolism of chemicals and the fixation of N (Wood 1989). The activity of soil organisms will influence the plant availability of micronutrients. The organisms, in turn, are influenced by a variety of soil, plant and environmental factors. For instance, Theodorou (1984) investigated the microbial properties of 5 soils under pine, eucalypt woodland and pasture. The results indicated that the type of vegetation significantly affected microbial numbers present in the soil, soil type and vegetation significantly affected soil microbial biomass N, and vegetation type significantly affected N transformations and mineral N but soil factors (e.g. temperature, moisture, total N%, and carbon:N of the organic matter) also influenced them.

2.6 TECHNIQUES USED TO ASSESS THE NUTRIENT STATUS OF TREES

The nutrient status of forests is measured via the analysis of both the soils in which the tree grows and the foliage it produces.

2.6.1 Soil analysis

Soil tests for Cu, Zn and B availability are not a standard part of forest soil analysis in New Zealand. Having foliage analysed for the content of these micronutrients is the method by which forest managers can assess their status in plantation trees. The general issue of sampling soil in forestry is complicated by soil heterogeneity and the number of samples required to represent the 'average' of a site, and the depths at which samples should be taken due to the deep rooting nature of trees compared to agricultural crops. However, prior to planting, and until the trees are several years old, soil testing is the only method available to predict nutrient availability. During the first few years of growth soil analysis for available micronutrients may give a useful indication of potential micronutrient problems (J.A. Adams and R.G. McLaren, unpublished).

While it is important that soil analysis attempts to measure a nutrient's availability to the plant and the soil's capacity to maintain a supply of that nutrient (Snowdon 1982), there are a number of difficulties associated with the use of soil chemical analysis to assess the nutrient supply in forests. For instance, a measurement of soil Cu availability will not be effective in predicting the plant uptake of Cu unless the amount of root exploitation of the soil is also accounted for (Jarvis and Whitehead 1981). Snowdon (1982) found a poor correlation between foliar B levels in radiata pine seedlings and hot-water soluble B in a range of Australian soils, except that deficiency did not occur at levels above 0.35μg B g^{-1}. Another aspect to be considered is that nutrient availability in the rhizosphere differs in many respects to the bulk soil around it (Marschner *et al.* 1987) and yet during the nutrient analysis of the soil it is mainly the bulk soil which is sampled.

In analysing the soil, those nutrient pools that directly supply the plant should be measured. As an example plants essentially respond to the soil solution B and therefore, it is this pool under field conditions that must be evaluated in determining B deficiency or toxicity (Gupta *et al.* 1985). Since B concentrations in surface soils are typically greater than below, the analysis of the surface horizons only will be satisfactory in many circumstances (Stone 1990).

2.6.2 Foliage analysis

Diagnosing micronutrient deficiencies has been difficult and the knowledge that currently exists about micronutrient nutrition and function within the plants is poor. For radiata pine, as noted by Hill and Lambert (1981), this information has often been extrapolated from other plant species. The reason for this, according to Turvey and Grant (1990), is the extremely refractory nature of conifer tissue which makes biochemical investigations difficult to carry out.

Foliar analysis in forestry has generally proved to be superior to soil testing for finding nutrient deficient areas (Ballard 1980) and also gives a direct measure of the nutrients that the plant has derived from the soil (Mead 1984). In New Zealand and Australia a great deal of research has been conducted in order to define what levels of nutrients should be in radiata pine foliage for healthy growth and the development of critical levels.

There is much ambiguity in the literature as to what a critical level, value or concentration represents in plant nutrition. Descriptions in the literature are frequently like that of Mengel and Kirby (1987) who describe the critical level as the point at which no further yield increase results from an increase in nutrient content or, as described by Mead (1984), the level below which a fertiliser response could be expected. According to Jones *et al.* (1991) the critical nutrient range (CNR) represents a range in concentration in which a 0 to 10% reduction in yield occurs. A 10% reduction in yield is specified as a nutrient's critical value.

'Critical' concentrations for micronutrients have been difficult to define due to the possibility of 1) the C-shaped relationships between growth and foliar concentrations of micronutrients and 2) the tree/environment interactions in symptom expression (Hill and Lambert 1981). A more reasonable approach is to consider ranges in concentrations of nutrients which indicate low, marginal and adequate levels (Mead 1984). This system is used to diagnose the nutritional status of radiata pine in New Zealand plantations (see Will 1985) but may not be appropriate for the genetically selected breed of radiata pine now being planted in ex-pasture systems where nutrient ratios and balances may be important in the diagnosis of nutritional problems.

As described by Stone (1990) the limitations of foliar analysis often go unrecognised and can lead to confusion where, for example, near the minimum range, concentrations in the foliage of apparently healthy trees may be lower than those in visibly deficient trees. Care is also required when selecting radiata pine foliage samples because, even within one season, the concentrations of B and Zn increase from oldest to youngest fascicles (Hill and Lambert 1981) and nutrient concentrations fluctuate with the time of sampling (Mead and Will 1976, Knight 1978).

Although significant relationships may exist between foliar nutrient concentrations and growth, the closeness of the correlation varies, indicating that the careful interpretation of foliar nutrient concentrations is required when using it as a guide for management decisions (Barker 1978). Sheriff *et al.* (1986) concluded that research into the physiological basis of nutrient use and reuse was necessary to define optimum tree nutrition and for refining the criteria for nutrient deficiency diagnosis in forestry plantations.

The effect of climate in influencing nutrient concentrations can be very important when assessing foliar nutrient concentrations. For B, for instance, there are problems in applying critical levels derived from one region to another (Mead 1984) presumably due to the important parameter of rainfall and the resulting soil moisture.

The nutritional problems experienced with growth syndromes in radiata pine in ex-pasture systems are unlikely to involve a single nutrient deficiency and are more likely to be the result of nutrient imbalances within the tree. The ratio between certain nutrients may mean more in this situation than single nutrient concentrations. When correlating tree growth with nutrient content, the implication of N imbalances with other nutrients suggests that ratios between N and these nutrients may prove useful. As an example, Turvey (1984) found that foliar Cu:N ratios were a more sensitive indicator of Cu fertiliser treatment than the concentrations of Cu or N alone.

There are other techniques that may be of use in diagnosing nutritional problems in ex-pasture systems. For instance, Van Dijk and Roelofs (1988) presented chemical composition relative to N (level as a % of N level) for Scots pine (*Pinus sylvestris* L.) and suggested that nutrient proportions could be more important than absolute levels. Also the Diagnosis and Recommendation Integrated Systems (DRIS) is a comprehensive diagnostic approach utilising the concept of nutrient balance and aims to obtain directly comparable indices for the factors which influence yield so that the relative adequacy or deficiency of each factor can be determined (Beaufils 1973). The indices are based on foliage nutrient ratios and include their variability. The advantage of DRIS is that the interrelationships of all the nutrients can be considered simultaneously (Schutz and de Villiers 1987). However, one of the difficulties of this technique, according to Truman and Lambert (1980), was the development of a general set of norms for radiata pine which they described as 'not possible'. According to Jones *et al.* (1991) there is not enough micronutrient concentration data in the literature to calculate DRIS norms and the questionable quality of data on micronutrient concentrations precludes the use of DRIS. Jones (1981) also noted that the complexity of the DRIS methodology had discouraged its use and suggested modifications to simplify its use and interpretation. Svenson and Kimberley (1988) suggested that the DRIS system could be used to complement conventional diagnostic methods.

Another nutrient diagnostic method is vector analysis. It is a graphical technique used to examine and diagnose shifts in response and forest stand nutrient status resulting from the addition of fertiliser (Weetman and Fournier 1982). The technique can produce response data and nutrient status diagnosis within one year of fertiliser application (Weetman and Fournier 1982). According to Binkley (1986) this technique should be evaluated for use with radiata pine and other conifer species which have multiple growth flushes each year.

2.6.3 The physical measurement of trees

2.6.3.1 Objective measurements

Physical measurement of the tree attributes yields data which can be compared objectively. Such measurements include height, diameter at breast height (DBH), basal area, branch diameter, needle lengths and component weights (e.g. of needles, branches, bark, stem etc.) where the trees are destructively harvested. Such measurements reflect a physical dimension of tree growth and, over time, will show particular growth responses to management techniques such as fertilisation, pruning and thinning.

Defining tree 'form' has not been a technique widely used in plantation forestry. Gordon and Graham (1986) studied the changes in radiata pine stem form in response to N and P fertiliser addition. Their data were based on the ratio of total stem volume to the volume under the bark but the measurements did not assess the deviations from a straight stem.

2.6.3.2 Subjective measurements

The description of visible symptoms is one of the most subjective and ambiguous methods for diagnosing nutrient deficiencies in plants (Turvey and Grant 1990). Once a nutrient deficiency manifests itself as a visual disorder, the damage to plant growth and metabolism has occurred and although the plant may recover with fertiliser additions, tree form and/or growth rates may have been reduced. Birk *et al.* (1989) noted that radiata pine established on ex-pasture country have developed form problems that have not been previously seen in radiata pine planted on non-pasture sites. The need to describe and measure these deformities has become an important requirement for assessing the quality and possible timber production from ex-pasture radiata pine plantings.

With speed wobbles, the visual symptoms have been the first indication of growth problems. Speed wobbles can be seen as a three dimensional change in tree form and often resembles a spiral (helix) in its manifestation in the new leader growth. Other aspects of poor form may include multiple leaders and heavy branching. The physical measurement of such deformities is both difficult and time-consuming. Thus researchers have tended to use subjective scales to reflect the severity of the growth malformations. For instance, Pederick *et al.* (1984) used a scale of malformation which went from 1 (no stem or branch deformation and minor stem kinks are disregarded) to 6 (complete deformation involving severe kinking, loops, or dead top of the leader and or branches). This system was also used by Hopmans (1990). Hopmans and Flinn (1991) used a simplified scale of 1 (straight) to 6 (severely deformed).

Pederick *et al.* (1984) noted that the main source of error in scoring was due to the inadequate view of the whole stem of some trees because of the dense foliage. J.A. Adams (pers. comm., 1992) suggested that a lack of experience in describing and categorising such growth malformations will affect how 'severe' the malformations are perceived to be. This was recognised by Birk *et al.* (1989) who stated that the assessment of tree form was limited to some extent by the subjectivity in the scoring of the severity of a defect but that the provision of photographs (as in their publication) reduced the variability between scorers and maximised comparability in terms of time and space. Birk *et al.* (1989) describe a comprehensive procedure for describing tree form in relation to leader stem and branch defects where scores in these categories produce the Growth Deformity Index (G.D.I.) and the Non-Utilisation Index (non-U.I.).

2.7 CONCLUSIONS

The nutrition of radiata pine in ex-pasture sites appears to be quite different from that of plantation forests, mainly due to the land-use history of the different sites. Nutrient processes in ex-pasture systems are complex due to the presence of the pasture component which competes with the trees for water and nutrients in the upper horizons of the soil profile. Other factors which may affect the availability and plant uptake of nutrients from the soil include climate (rainfall), topography, tree genetics, soil chemical and physical properties, tree root development, mycorrhizal associations, the characteristics of the rhizosphere, soil microorganisms and the addition of fertilisers.

The development of growth deformities in radiata pine growing in ex-pasture soils appears to be widespread and can severely affect wood production. Recent research indicates high levels of soil N, particularly in the nitrate form, and a sites high potential to nitrify as important factors that may affect the nutritional balance of radiata pine and cause stem deformities.

In ex-pasture systems the assessment of radiata pine nutrition may require visual assessment for stem deformities and the measurement of foliar nutrient ratios and balances, particularly in relation to N.

Chapter 3

The Taheke field trial: Effect of N addition on the nutrient concentrations and physical growth of young radiata pine and on the soil N levels in an ex-pasture system.

3.1 INTRODUCTION

High levels of N, particularly in the form of nitrate, have been implicated in the development of radiata pine growth deformities in ex-improved pasture sites (Carlyle *et al.* 1989, Birk 1990, Hopmans and Flinn 1991). These deformities have been especially severe on improved legume pastures with high nitrification potential (Hopmans and Flinn 1991, Birk *et al.* 1991). Very high risk sites for potential growth problems and resulting poor form include cleared improved pastures on soil derived from igneous rocks (Birk *et al.* 1991). The deformities include lack of apical dominance, heavy branching and bent and twisted stems (Birk 1990) and are known as the "Toorour Syndrome" (Carlyle *et al.* 1989, Turvey and Grant 1990), "Speed Wobbles" (Will 1986, Shoemark 1988, Will 1990) and "poor form" (Birk 1990).

The addition of N fertiliser has been shown to increase tree deformities and reduce growth rates (Birk *et al.* 1991, Downes and Turvey 1986) particularly on soils of low to moderate fertility (Woods 1982, Hopmans and Flinn 1991) and ex-pasture soils (Birk *et al.* 1991). Although the role of nitrate-N in causing radiata pine growth deformities on ex-improved pasture is not fully understood it appears that the presence of high nitrate-N levels creates an imbalance between N and other essential nutrients (Birk *et al.* 1991, Turner and Lambert 1991) such as B, sulphur (S) and phosphate, which are absorbed as anions (Birk *et al.* 1991). For radiata pine in conventional forests, high soil N levels or the application of N fertilisers have induced deficiencies of Cu (Will 1971, Turvey and Grant 1990, Hunter *et al.* 1990a), Zn (McGrath and Robson 1984, Boardman and McGuire 1990a) and B (Lambert and Turner 1977).

In the typically acid soils of mature forests, ammonium is thought to be the predominant form of inorganic N available for plant uptake (Attiwill and Leeper 1987). In contrast, in pasture sites nitrate is usually the main form of inorganic N with ammonium-N present at only low amounts (Adams 1986). The pathway of nitrification, through the conversion of ammonium via nitrite to nitrate (Attiwill and Leeper 1987), may occur autotrophically by the nitrifying bacteria such as *Nitrosomonas* and *Nitrobacter* (Focht and Verstraete 1977). Alternatively, heterotrophic nitrification can be of quantitative significance in acid environments (Adams 1986) where nitrate-N production would be expected to be related to the amount of organic-N present (Focht and Verstraete 1977). One of the major determinants of the type of nitrification pathway that may occur at a given site is soil pH. Duggin *et al.* (1991) showed that at pH 3.5 nitrification in fresh forest floor samples, from a Northern hard wood forest, was solely heterotrophic while at pH 6.6 it was solely autotrophic. They found that the quality of the forest floor material, i.e the ratio of recalcitrant to easily decomposable compounds, was also an important factor determining the nitrification pathway. In pastoral ecosystems, where pH values are optimally 5.4 to 6.0 (During 1984), and there is a high proportion of readily metabolisable energy sources, autotrophic nitrification is likely to be the major source of nitrate. As the acidity of forest soils does not provide conducive conditions for autotrophic nitrification (Keeney 1980) the occurrence of nitrification in these systems suggests that a heterotrophic pathway for nitrate-N production could exist (Adams 1986).

Carlyle *et al.* (1989) found that soils under pasture showed higher rates of N mineralisation, especially nitrification, than ex-eucalypt soils. Hopmans and Flinn (1991) found a strong correlation between stem deformity, in 6 year-old radiata plantations on pasture sites, and the soils potential nitrification as measured by aerobic laboratory incubations. To distinguish between the nitrification pathways, substrate amendment techniques have been used. The addition of ammonium N to the soil stimulates bacterial growth and inhibits or has no effect on nitrification in samples which nitrify heterotrophically (Focht and Verstraete 1977).

The stem deformities of radiata pine have generally been measured subjectively by visual assessment (e.g. Pederick *et al.* 1984, Hopmans and Flinn 1991). In categorising stem deformities large errors can arise from an inadequate view of the whole stem (Pederick *et al.* 1984), lack of experience and perception of the severity of the malformation (J.A. Adams, pers. comm. 1992) and the three dimensional nature of the deformities. Standardisation, such as the photographic publication of Birk *et al.* (1989) will reduce variation between scorers and clarify the type and severity of the stem deformities observed.

The aim of this study was to investigate the effect of adding large amounts of N on foliar nutrient concentrations and ratios - particularly those of N with the micronutrients Cu, Zn and B - and to attempt to enhance a visually mild case of the speed wobbles syndrome in a young agroforest of radiata pine. It was hypothesised that both the number of trees exhibiting the syndrome and its severity would increase over the growing season and that such changes could be correlated with foliar nutrient concentrations and ratios and soil N characteristics.

In the ex-pasture soils of the Taheke agroforest site it was hypothesised that, due to the history of pasture maintenance and the only recent establishment of a radiata pine agroforest, nitrification would be via an autotrophic pathway. An aerobic incubation study was therefore undertaken to compare the nitrification pathway operating in the agroforest soils, two adjacent pasture sites and a mature conventional stand of radiata pine.

3.2 MATERIALS AND METHODS

3.2.1 Site descriptions

During August of 1989 a field trial was set up in a young plantation of radiata pine growing on an ex-pasture site, known as 'Taheke' and owned by Tasman Forestry Limited, situated 20km north east of Rotorua approximately 10km from Rotorua Airport (**Figure 3.1**). The terrain was undulating and tree spacing was 2m within the rows and an average of 2.5m between the rows (range was 2.0 to 3.3m) resulting in an average stocking rate of 2000 stems per hectare. The trial area (described as the Taheke ex-pasture site in this chapter) was not grazed and the vegetation was rank grass which was being slowly invaded by weed species such as blackberry. The farming history of this ex-pasture site is unknown.

Two pasture sites (described as Taheke pasture site 1 and Taheke pasture site 2) adjacent to the Taheke ex-pasture trial site, and a site in Whakarewarewa Forest were also soil sampled . The Taheke pasture sites were grazed by sheep and cattle. The farming history of this ex-pasture site is unknown. The Whakarewarewa Forest is located just south of Rotorua and is approximately 9km from Rotorua Airport. The site that was sampled was a second rotation mature radiata pine stand in compartment 20.

The soils in the Taheke area were described by Rijkse (1979) as a complex of Oturoa hill soils (composite yellow-brown pumice from rhyolitic tephra) and Pohaturoa steepland soils (steepland soils related to composite soils from rhyolitic tephra on ignimbrite). In Whakarewarewa Forest the soil was a Haparangi sandy loam (composite yellow-brown pumice soil on yellow-brown loam, Rijkse 1979).

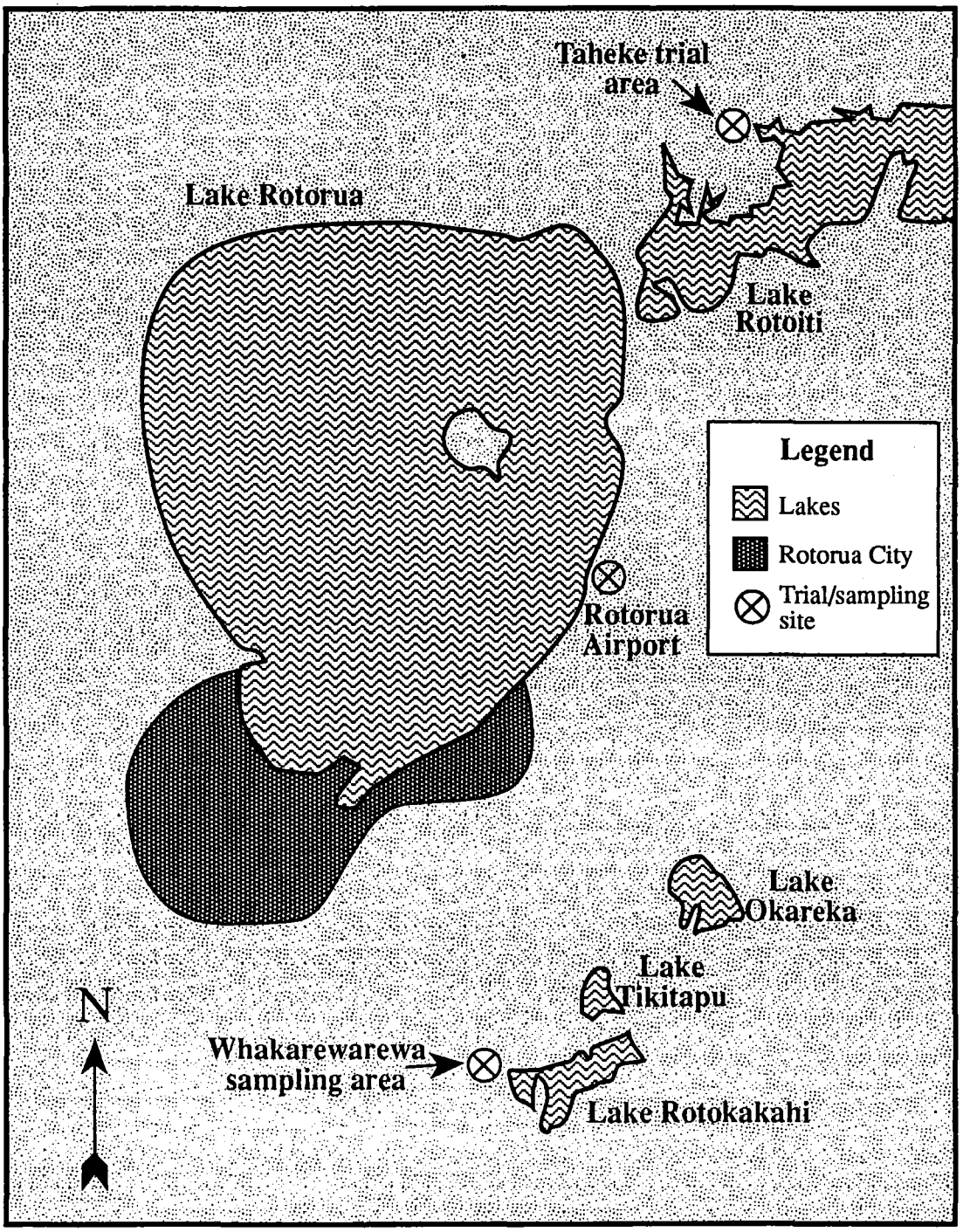

Figure 3.1: Map of the Rotorua area showing the location of the Taheke trial site (ex-pasture and pasture), the Whakarewarewa Forest sampling area and Rotorua Airport. Not to scale.

3.2.2 Taheke ex-pasture trial design

The trial at the Taheke ex-pasture site consisted of 3 N treatments randomly applied as urea (46% N) at 0, 250, and 500kg N ha^{-1} and replicated four times. The plots were randomly located across the trial area and the fertiliser treatments were broadcast manually. Each plot was 4m wide and a variable length (18.5-27.5m) to contain ten trees in a row. The trial covered an area of approximately 0.25 ha.

3.2.2.1 Foliage sampling and analysis

Foliage samples, of the current season's fully extended needles from the second order branches in the top third of the crowns, were taken from 5 randomly chosen trees per plot in August (prior to the addition of the fertiliser), October and December of 1989, and in February 1990 from the radiata pine trees growing on the Taheke ex-pasture site. The samples were placed in paper bags, dried at 70°, ground (1mm), and stored in plastic containers prior to analysis for their nutrient contents.

Levels of N, P, K, Ca, and Mg were measured following a H_2SO_4/H_2O_2 digestion with the N and P levels measured on an auto-analyser and K, Ca, and Mg on an atomic absorption spectrophotometer as described by Nicholson (1984).

Micronutrient (Cu, Zn and B) levels were measured using a dry ashing technique where 1.00g of ground foliage sample was weighed into a silica crucible, placed in a cold muffle furnace, heated to 600°C and ashed for 1 hour. When cool, 10ml of 0.5M H_2SO_4 was added to extract the ash for 1 hour at room temperature. The solution was filtered (Whatman 40) into a plastic vial. Cu and Zn levels were measured on the atomic absorption spectrophotometer (Shimadzu AA-670) and B levels were found using the azomethine-H method (Wolf 1974, Gaines and Mitchell 1979).

The nutrient:N ratios were calculated as follows:

$$\frac{Macronutrient\ (mg\ g^{-1})\ or\ micronutrient\ (\mu g\ g^{-1})}{Nitrogen\ (mg\ g^{-1})}$$

3.2.2.2 Physical tree measurements

Tree heights (using height poles), DBH (at 1.3m with a measuring tape), and a visual assessment of stem deformity were taken in August 1989 and February 1990. The distribution of stem deformity in August, prior to fertiliser application, is shown in **Figure 3.8**.

The trees were visually graded as to the number of the kinks that were present in the new growth of the main leader of each tree. The sum of each kinks' severity[1] was used to calculate the level of stem deformity per tree. February assessments were made on the leader growth since August.

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[1] The severity or size of the kink was expressed in terms of the number of tree diameters (at the mid-point of the kink) that the kink deviated from the overall centre line of the tree if it were growing straight.

3.2.3 Soil sampling and analysis

3.2.3.1 Sampling

In August 1989 (prior to fertiliser application) and February 1990, 10 soil cores, from the 0 to 10 cm and 10 to 20 cm depths, were taken from each of the 12 plots at the Taheke ex-pasture trial site, north of Rotorua, and from two adjacent pasture sites (Taheke pasture sites 1 and 2). The cores from each Taheke plot and the cores from the other sites were bulked according to depth.

Ten soil core samples, from 0 to 10 and 10 to 20cm depths, were also taken from the site in Whakarewarewa Forest.

The cores were kept in a moist condition in sealed plastic bags at 4°C.

3.2.3.2 Aerobic incubations

An aerobic incubation was used to assess the nitrification potential of the August soil samples from the 0-10cm depth. Twenty five grams of moist soil (in duplicate) were placed in a plastic pottle and bought to 80% field capacity by the addition of 3ml of distilled water (control) or 3ml of ammonium sulphate $(NH_4)_2SO_4$ solution to give 250μg N g^{-1} of OD soil (amended). The pottles were covered (the lids had a 1mm air hole) and incubated for 21 days at 25°C. The samples were then shaken end-over-end for 1 hour with 125ml of 1M KCl, filtered (Whatman 42) and refrigerated prior to analysis for NO_3^--N (Kamphake *et al.* 1967) and NH_4^+-N (Weatherburn 1967). Soil samples, at 80% field capacity, were also extracted with 125ml of KCl (as described above) at Day 0 to find the initial levels of nitrate-N and ammonium-N.

3.2.3.3 Anaerobic incubation

An anaerobic incubation, based on the method of Keeney and Bremner (1966) as described by Selvarajah *et al.* (1987), was used to estimate the levels of potentially mineralisable N (described in this chapter as 'mineral-N') present in the soil samples collected from both depths (0-10 and 10-20cm) in August and February. Duplicate 5.0g sub-samples of moist soil were placed in plastic specimen jars. Ten ml of distilled water was added and the suspension stirred to release any trapped air bubbles. The jar was then sealed and placed in an incubator cabinet at 40°C for 7 days. After the incubation, 10ml of 2N KCl was added to the samples which were then shaken for 1 hour end-over-end, filtered (Toyo 5C) and refrigerated until analysed for NH_4^+-N on the auto-analyser (Weatherburn 1967).

After the incubation studies were completed the remaining soil in each sample was air-dried and sieved (2mm).

3.2.3.4 Total N

Total N, in air-dried soil samples from depths of 0-10 and 10-20cm (collected in August and February), was determined after a Kjeldahl digestion (Nicholson 1984) by analysis for NH_4^+-N using an Autoanalyser (Weatherburn 1967).

3.2.4 Soil profiles

3.2.4.1 Sampling

Four soil profiles were studied. Two of these were within the ex-pasture trial area (Taheke ex-pasture 1 and 2), one was in a nearby pasture (Taheke pasture site 2), and the other in Whakarewarewa State Forest. Each profile was divided into its visible horizons, the horizon depths were measured and a description of soil structure, colour, texture, and the presence of plant roots and volcanic lapilli was made. A representative soil sample was taken from each horizon of each soil profile. The samples were then air-dried, and sieved (2mm).

3.2.4.2 Analysis

The profile soil samples were analysed for pH, % of organic carbon (C), total N%, Bray 2 P, and Bray 2 K, Ca and Mg according to the methods described by Nicholson (1984).

3.2.5 Statistics

Data were subjected to analysis of variance (ANOVA) using the computer program GENSTAT. The following effects were examined:

(i) The effect of the increasing rates of N on the control foliar nutrient concentrations for the effect of sampling date.
(ii) The effect of the increasing rates of N on foliar nutrient concentrations and nutrient:N ratios from October to February.
(iii) The effect of the increasing rates of N on the tree physical measurements of height, DBH and stem deformity.

The Least Significant Difference (LSD) test was used to compare mean values.

The regression coefficient (r) was calculated for each of the following paired observations using the computer program STATVIEW:
(i) Physical tree measurements and foliar concentrations.
(ii) Physical tree measurements and soil N characteristics.
(iii) Foliar nutrient concentrations in the control plots and rainfall in the month prior to sampling.

3.3 RESULTS

3.3.1 Climate

The climate data were from Rotorua Airport which was the nearest meteorological station (New Zealand Meteorological Service 1989, 1990).

Monthly rainfall during the trial period was below normal except for the months of September and October (**Figure 3.2**). The October rainfall at 265mm was more than twice the normal 116mm. December was particularly dry with a rainfall of 40mm compared to the normal 138mm. It should be noted that the Taheke trial site was in a different rainfall isohyet than Rotorua Airport (Rijkse 1979). At Rotorua Airport the annual rainfall is between 1600 and 2000mm compared to Taheke at 2000 to 2400mm.

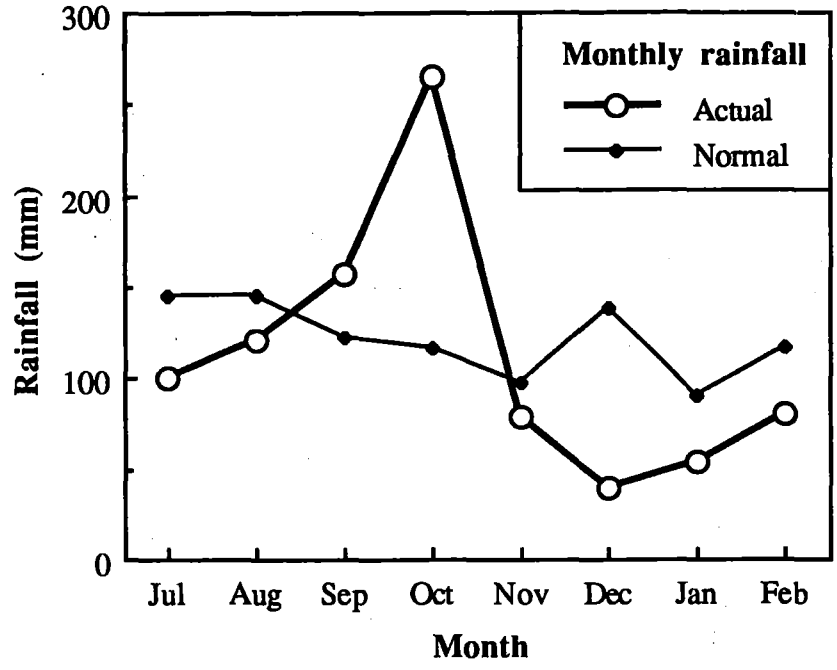


Figure 3.2: Total and normal monthly rainfall from July 1989 to February 1990 at Rotorua Airport.

Mean air temperatures were generally warmer than normal from August 1989 to February 1990 **(Figure 3.3)**.

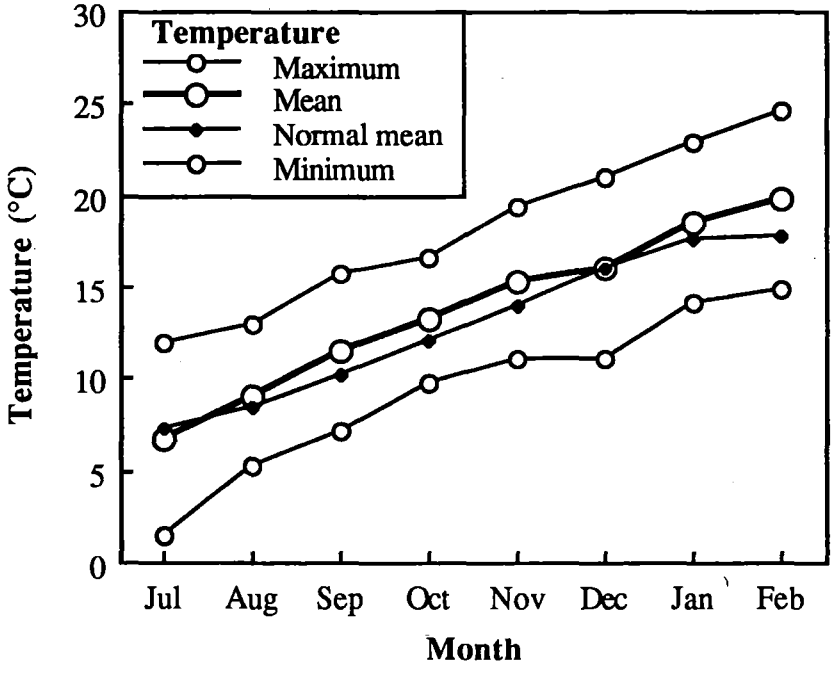


Figure 3.3: Air temperatures from July 1989 to February 1990 at Rotorua Airport.

3.3.2 Nutrients in the radiata pine foliage

3.3.2.1 Nutrient concentrations prior to fertiliser addition

Prior to the addition of the N fertiliser in August there was a difference between plots in the foliar concentrations of N and K (**Figure 3.4**). The average concentrations of these nutrients were significantly ($p<.05$) higher in the plots that were to receive 250kg N ha^{-1} than in those plots that were to receive 500kg N ha^{-1}.

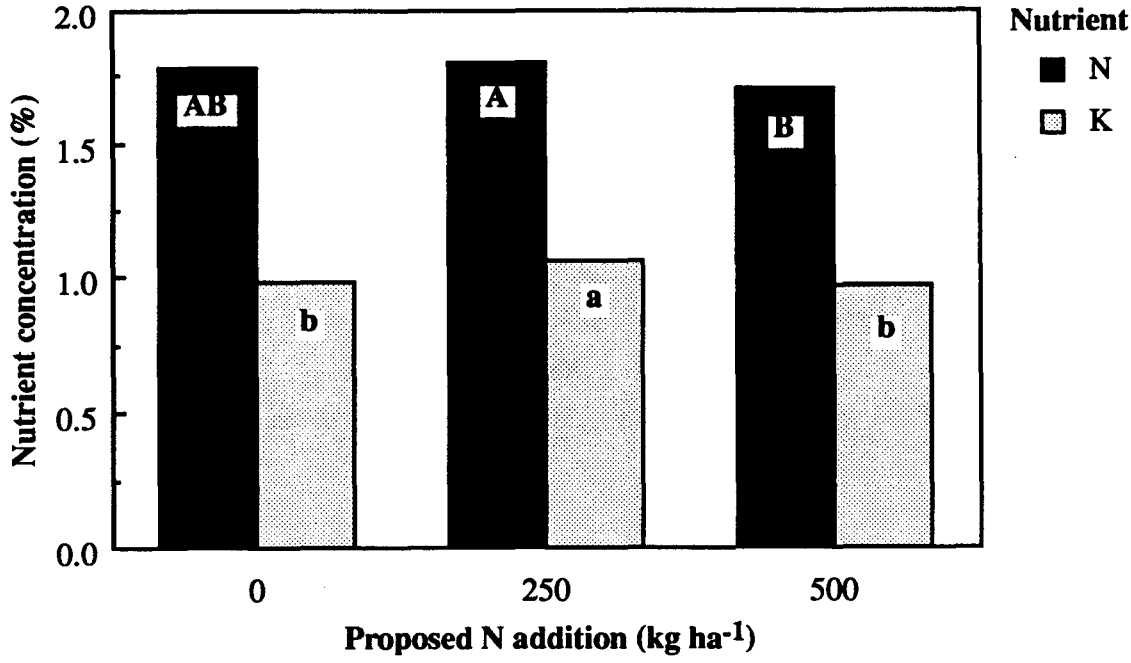


Figure 3.4: Radiata pine foliar concentrations of N and K in the treatment plots prior to urea-N addition, in August, at Taheke. For each nutrient, means with the same letter were not significantly different ($p<.05$).

3.3.2.2 Changes in nutrient concentrations of the control plots with sampling date

From August to February, the effect of sampling date was highly significant ($p<.001$) on the foliar concentrations of N, P, K, Ca and B and significant ($p=.018$) for Zn in the control (N_0) plots (**Table 3.1**). Apart from N and B, whose concentrations were significantly ($p<.05$) lower in February, the nutrient concentrations displayed different patterns of change with sampling date. The foliar P concentrations were significantly higher in December than at the other sampling dates. In October, the K concentration was significantly lower, while Ca concentrations were significantly higher, than during the other sampling dates. The concentration of Zn was significantly higher in October than in December and February.

The amount of rainfall in the month prior to foliage sampling at Taheke was significantly correlated with the concentrations of Ca ($p=.057$) and Zn ($p=.046$) in the control plots (**Figure 3.5**) from August to February. As the amount of rainfall increased so did the foliar concentrations of both Ca and Zn.

Table 3.1: The mean concentration of nutrients in radiata pine foliage in the control plots at each sampling date at Taheke.

	August	October	December	February
N %	1.78 a*	1.76 a	1.77 a	1.62 b
P %	0.142 b	0.135 b	0.176 a	0.135 b
K %	0.99 b	0.81 c	1.17 a	1.06 ab
Ca %	0.224 b	0.303 a	0.177 c	0.192 bc
Mg %	0.085 a	0.080 a	0.074 a	0.075 a
Cu $\mu g\ g^{-1}$	4.3 a	4.0 a	4.0 a	4.2 a
Zn $\mu g\ g^{-1}$	46 ab	48 a	41 b	39 b
B $\mu g\ g^{-1}$	16.8 a	15.4 a	16.0 a	11.4 b

* For each nutrient, means followed by the same letter were not significantly different ($p<.05$).

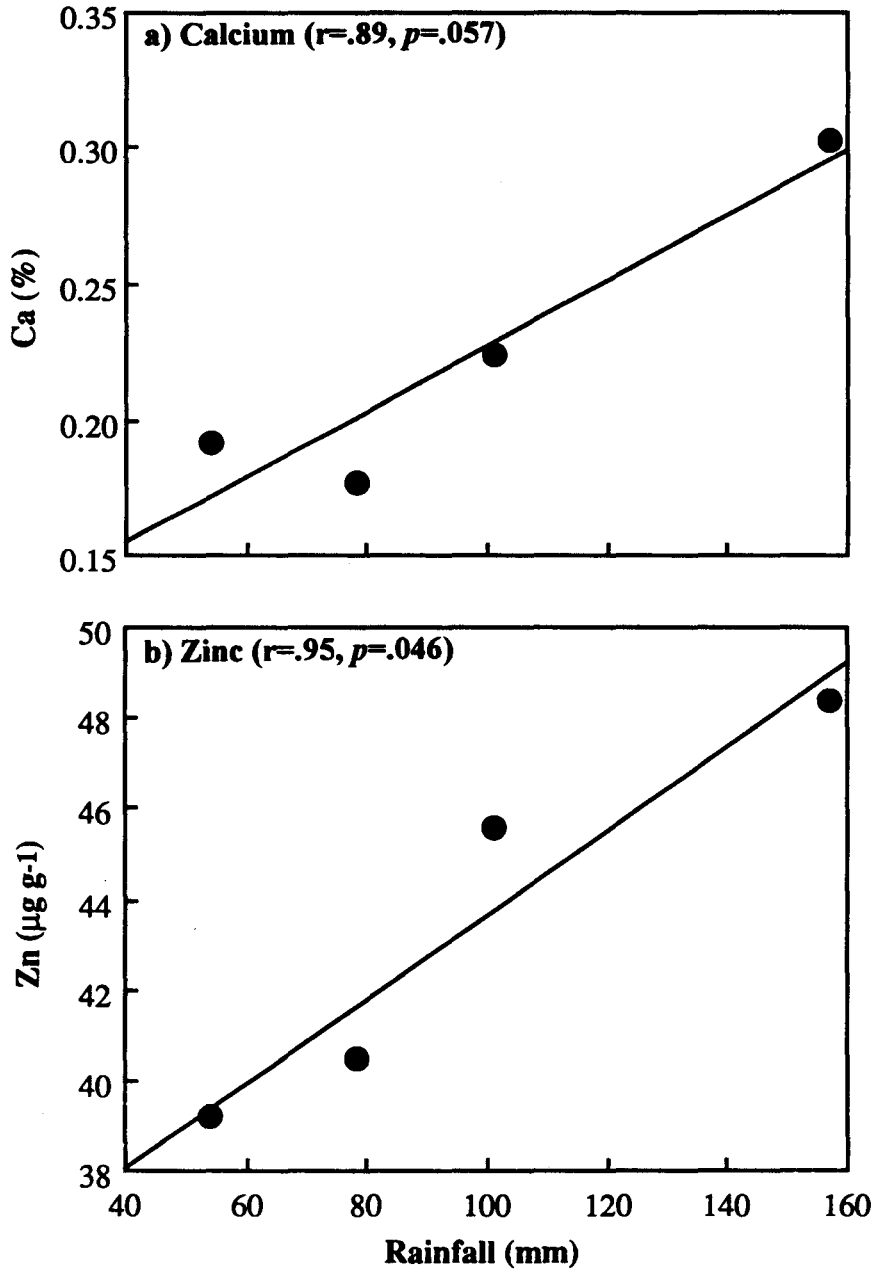


Figure 3.5: Significant correlations between radiata pine foliar nutrient concentrations in the control (N_0) plots and rainfall at Rotorua Airport in the month prior to sampling at Taheke ex-pasture site.

3.3.2.3 Effect of added N on nutrient concentrations

The addition of N had a significant effect on the concentrations of N, P, Ca, Mg, and Cu at different sampling dates from October to February.

The addition of N at 500kg ha^{-1} (N_{500}) significantly increased N% in the foliage to 1.87% compared to the control (N_0) level of 1.76% in October (**Table 3.2**). In December and February there were no significant differences between the rates of N addition.

Increasing rates of N addition resulted in a decrease in P% (**Table 3.2**). In December the difference between the control and the N treatments was significant. By February, there was no significant difference between the N_0 and N_{250} treatments, but for N_{500} the P level of 0.110% was significantly lower than the N_0 concentration of 0.135%.

Throughout the trial the Ca concentrations were relatively high (**Table 3.2**) compared to the standard foliar values described by Will (1985). In December, when Ca% was at its lowest, the addition of N_{250} and N_{500} resulted in Ca concentrations of 0.140% and 0.138% respectively which were significantly lower than the N_0 level of 0.177%. The correlation between Ca concentrations and rainfall in the month prior to foliage sampling from October to February for all N additions were not significant.

In December the addition of N_{250} resulted in a Mg concentration of 0.065% which was significantly ($p<.05$) lower than the 0.074% Mg recorded for the N_0 plots.

Copper concentrations showed a positive response to N additions in October. At N_{500} the Cu concentration of 4.4μg g^{-1} was significantly greater ($p<.05$) than the N_0 level of 4.0μg g^{-1}. From October to February the concentrations of Cu were significantly correlated with rainfall in the previous month for the N_{250} treatment only (**Figure 3.6**).

The concentrations of Zn, while not significantly affected by N addition, were significantly correlated with the amount of rainfall in the month prior to sampling (**Figure 3.7**).

In February, those nutrient concentrations that were satisfactory according to standard values (Will 1985) were N, K, Ca, and Zn (**Table 3.2**). The concentrations of P and Mg were marginal, at 0.14% and 0.08% respectively, in the N_0 treatment. The concentration of P in the N_{500} treatment was low at 0.11% while the concentration of Mg was low (0.07%) in both the N_{250} and N_{500} treatments. Copper concentrations were marginal, at 3.8μg g^{-1}, for the N_{250} treatment and B was marginal in all of the N treatments with concentrations ranging from 10.7 to 11.4μg g^{-1}.

3.3.2.4 Effect of added N on nutrient:N ratios

The addition of N had a significant effect on some of the nutrient:N ratios from October to February. The N_{500} treatment resulted in P:N ratios significantly less ($p<.05$) than the control from October to February (**Table 3.3**). The N_{250} treatment significantly depressed the P:N ratio in December.

In December both N treatments significantly ($p<.05$) reduced the Ca:N ratio. The Mg:N ratios were also reduced by N addition - significantly ($p<.05$) for N_{250} at 0.035 compared to the control of 0.042.

The N_{250} treatment significantly ($p<.05$) reduced the Cu:N ratios in February.

Table 3.2: Effect of added N on radiata pine foliar nutrient concentrations from October 1989 to February 1990 at the Taheke ex-pasture site and the probability (p) of a significant N main effect.

	Added N (kg ha^{-1})	October	December	February
			--- % ---	
N	0	1.76 b*	1.77 a	1.62 a
	250	1.82 ab	1.86 a	1.64 a
	500	1.87 a	1.83 a	1.64 a
		p = .013		
P	0	0.135 a	0.176 a	0.135 a
	250	0.130 a	0.156 b	0.129 ab
	500	0.128 a	0.154 b	0.110 b
			p = .053	p = .044
K	0	0.81 a	1.17 a	1.06 a
	250	0.81 a	1.22 a	1.06 a
	500	0.81 a	1.17 a	0.99 a
Ca	0	0.303 a	0.177 a	0.192 a
	250	0.291 a	0.140 b	0.162 a
	500	0.329 a	0.138 b	0.170 a
			p = .021	
Mg	0	0.080 a	0.074 a	0.075 a
	250	0.074 a	0.065 b	0.068 a
	500	0.082 a	0.067 ab	0.068 a
			p = .078	
			--- µg g^{-1} ---	
Cu	0	4.0 b	4.0 a	4.2 a
	250	4.2 ab	3.9 a	3.8 a
	500	4.4 a	4.0 a	4.0 a
		p = .033		
Zn	0	48 a	41 a	39 a
	250	46 a	38 a	37 a
	500	47 a	38 a	37 a
B	0	15.4 a	16.0 a	11.4 a
	250	14.1 a	16.4 a	10.7 a
	500	14.9 a	15.6 a	11.3 a

* For each nutrient concentration, within a sampling date, values followed by the same letter were not significantly different (p<.05).

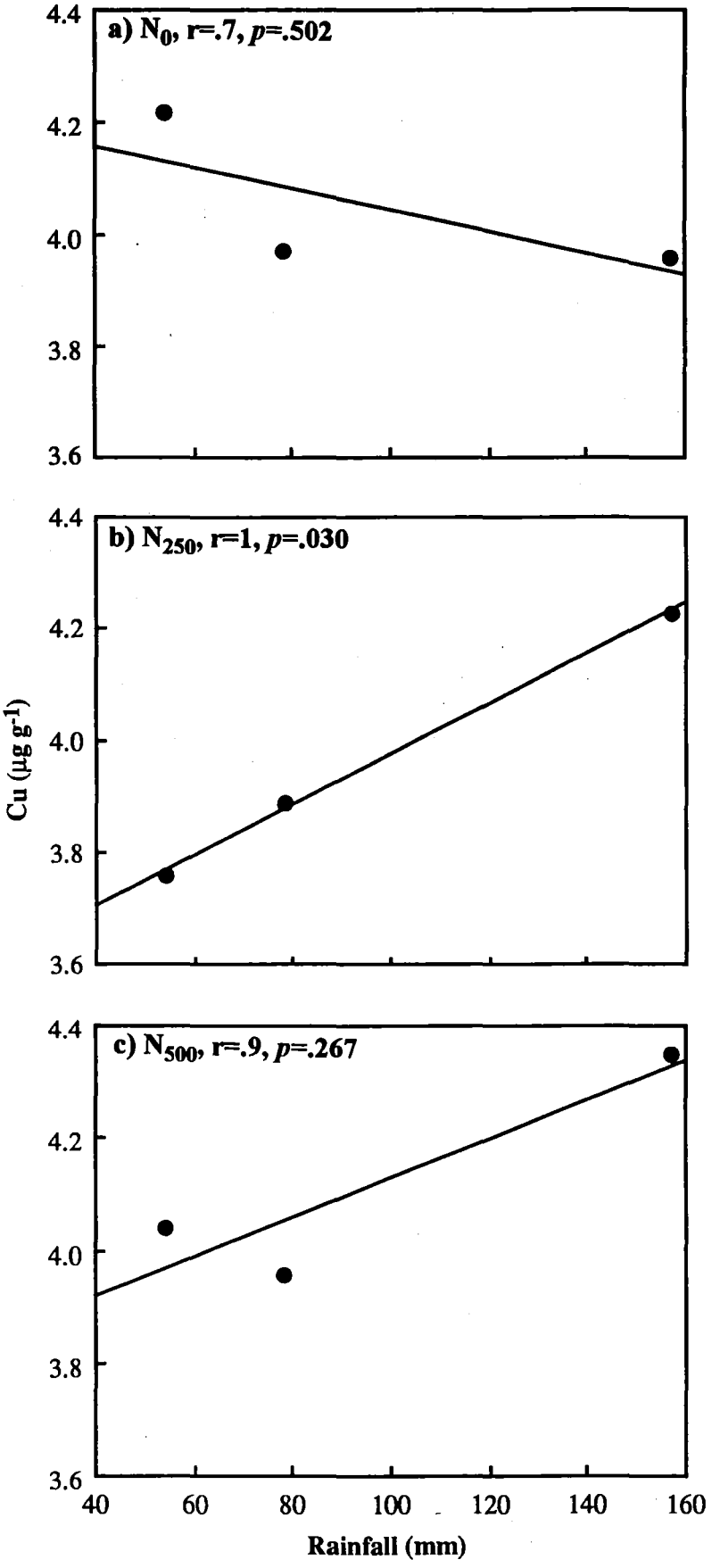


Figure 3.6: Correlations between radiata pine foliar Cu concentrations, at three rates of added N, and rainfall at Rotorua Airport in the month prior to sampling.

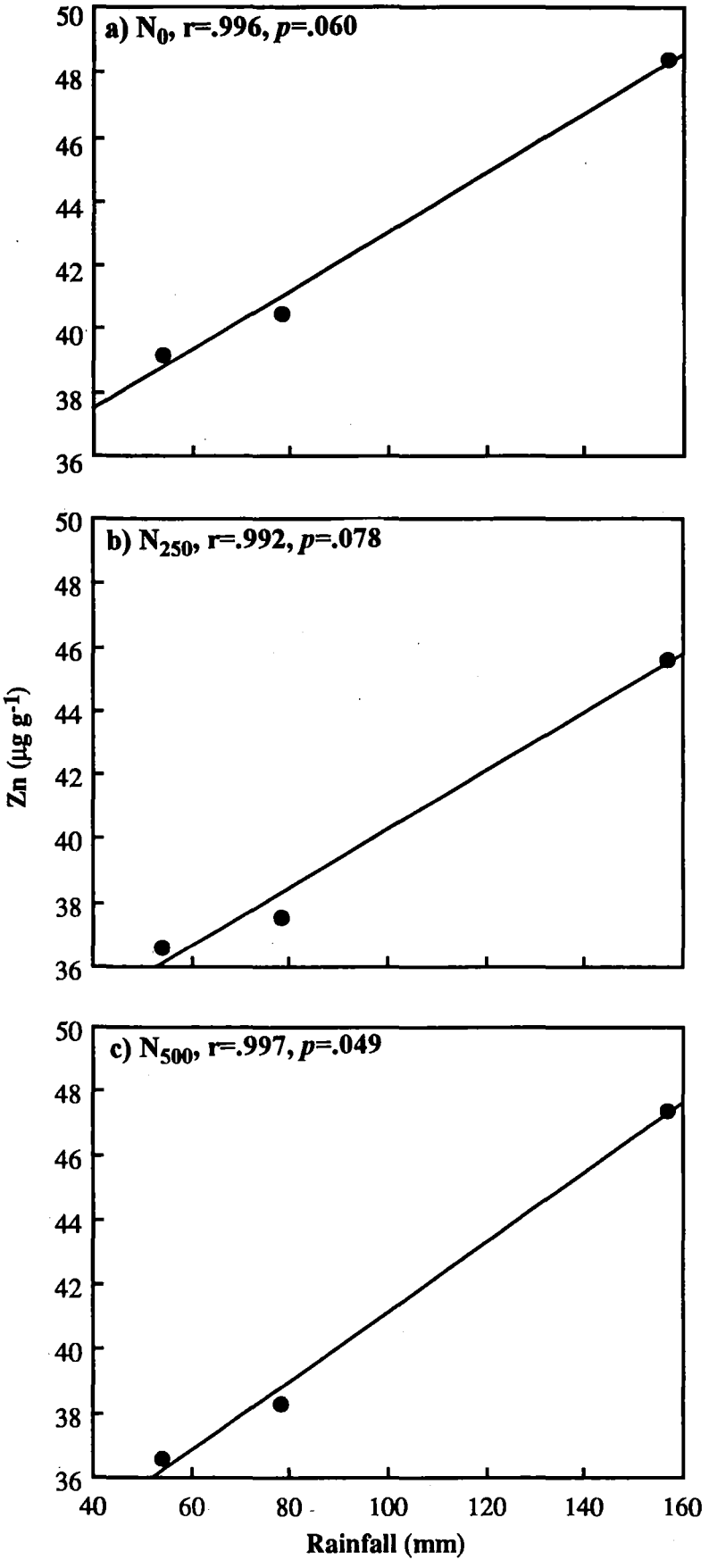


Figure 3.7: Correlations between radiata pine foliar Zn concentrations, at three rates of added N, and rainfall at Rotorua Airport in the month prior to sampling.

Table 3.3: Effect of added N on radiata pine foliar nutrient:N ratios from October 1989 to February 1990 at the Taheke ex-pasture site and the probability (p) of a significant N main effect.

	Added N (kg ha^{-1})	October	December	February
P:N*	0	0.077 a#	0.100 a	0.083 a
	250	0.071 ab	0.085 b	0.079 a
	500	0.069 b	0.084 b	0.067 b
		p = .042	p = .003	p = .010
K:N	0	0.46 a	0.66 a	0.66 a
	250	0.44 a	0.62 a	0.65 a
	500	0.43 a	0.64 a	0.61 a
Ca:N	0	0.17 a	0.101 a	0.12 a
	250	0.16 a	0.075 b	0.10 a
	500	0.18 a	0.078 b	0.10 a
			p = .018	
Mg:N	0	0.046 a	0.042 a	0.046 a
	250	0.041 a	0.035 b	0.042 a
	500	0.044 a	0.037 ab	0.042 a
			p = .032	
Cu:N	0	2.3 a	2.3 a	2.6 a
	250	2.3 a	2.1 a	2.3 b
	500	2.3 a	2.2 a	2.5 ab
				p = .074
Zn:N	0	28 a	23 a	24 a
	250	25 a	20 a	22 a
	500	25 a	21 a	22 a
B:N	0	8.8 a	9.0 a	7.0 a
	250	7.7 a	8.8 a	6.5 a
	500	8.0 a	8.5 a	6.9 a

For each nutrient:N ratio and month, means followed by the same letter were not significantly different (p<.05).

3.3.3 Tree growth

The trees grew substantially during the trial. From August to February the average tree height increased from 3.8 to 5.3m and the diameter from 7.4 to 11.0cm. However, by February the addition of N had not significantly affected mean tree diameter or height measurements or influenced any of the changes in these measurements. Using the August tree heights and diameters as respective covariates for the February measurements of height and diameter explained much of the variation in the Anova sums of squares (90 and 80% respectively).

The number of trees unaffected by stem deformities decreased from 38 in August to 15 in February (**Figure 3.8**). The number of trees with a small amount of stem deformity - from 0.5 to 1.5 - declined from August to February while the number of trees with stem deformity levels greater than 1.5 generally increased. While stem deformity had worsened during the trial, the addition of N had no significant effect on the levels of stem deformity or the number of kinks measured in the stem growth from August to February.

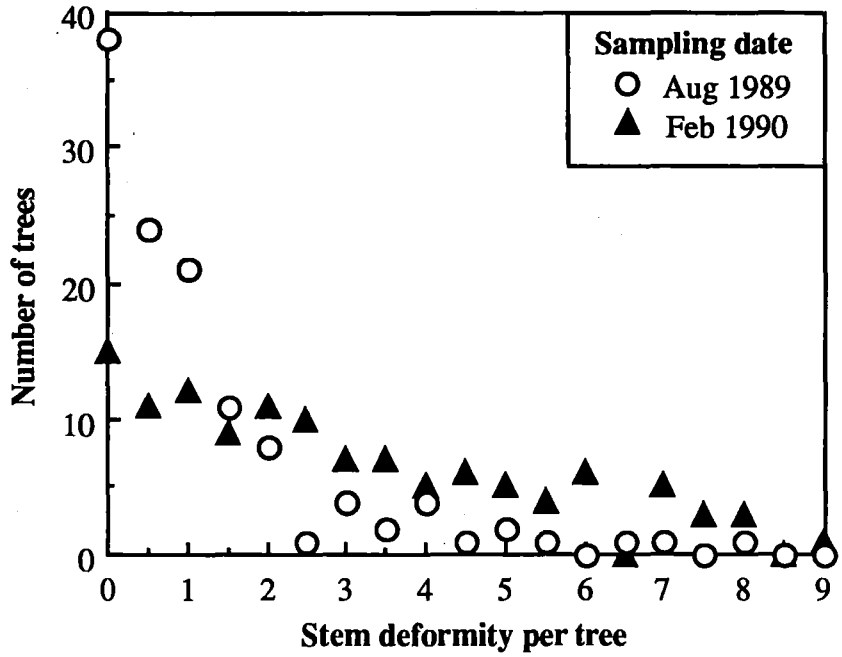


Figure 3.8: Distribution of radiata pine numbers in stem deformity categories at two sampling dates at the Taheke ex-pasture site.

3.3.4 Correlations between foliar nutrient levels and tree growth characteristics

The August foliar concentrations of N, P and Zn were significantly and positively correlated with August tree height (**Table 3.4**). Tree height was also significantly correlated with P:N, Ca:N, Mg:N, and Zn:N ratios. Tree heights increased as both P:N and Zn:N ratios increased but as Ca:N and Mg:N ratios increased mean tree height decreased. There were no significant correlations between foliar nutrient concentrations or nutrient:N ratios and the level of stem deformity or the number of kinks per tree measured in August.

In February, stem deformity was positively and significantly correlated with both N and Zn concentrations in the foliage (**Table 3.4**). The Cu:N ratios were significantly correlated with the mean number of kinks per plot. As the Cu:N ratio increased, the number of kinks decreased.

3.3.5 Soil cores

3.3.5.1 Aerobic incubation

The amounts of ammonium-N measured at Day 0 were similar and extremely low for all four sites (**Table 3.5**). Nitrate-N levels ranged from 0.0, for the Whakarewarewa Forest site, to 40.9 $\mu g\ g^{-1}$ for the Taheke pasture site 1. By subtracting the amounts of nitrate-N and ammonium-N measured

at Day 0 from the respective amount measured after the 21 day incubation, the changes in the amounts of nitrate-N and ammonium-N due to the substrate amendment, could be calculated. For the control treatment (i.e. 0μg N added g^{-1} OD soil) nitrate was the dominant form of N in the Taheke ex-pasture and pasture sites, and ammonium was the dominant form in the Whakarewarewa Forest site (**Figure 3.9**). Amendment with $(NH_4)_2SO_4$ increased nitrate production the most in the Taheke ex-pasture samples - from 32 μg g^{-1} to 125 μg g^{-1} where nitrate was again the main form of N at the Taheke ex-pasture site and the Taheke pasture site 1. At both sites, the $(NH_4)_2SO_4$ amendment promoted the production of nitrate while ammonium-N levels were reduced from the 250 μg g^{-1} added.

Table 3.4: Significant linear relationships between plot means of radiata pine physical measurements and foliar nutrient concentrations and nutrient:N ratios, at the Taheke ex-pasture site in August 1989 and February 1990, and the significance (probability level) of the relationship.

Tree growth characteristic	Foliar nutrient concentration/ratio	Regression coefficient (r)	Probability level
August:			
Tree height	N	.63	.028
	P	.74	.006
	Zn	.72	.009
	P:N	.59	.045
	Ca:N	-.63	.029
	Mg:N	-.56	.060
	Zn:N	.58	.048
February:			
Stem deformity	N	.62	.033
	Zn	.63	.030
No. of Kinks	Cu:N	-.61	.037

Table 3.5: Amount of ammonium-N and nitrate-N extracted from the August soil core samples (0-10cm depth) from the four sites at Day 0. The Taheke ex-pasture results are means from 12 plots (ranges in brackets).

Site	Ammonium-N	Nitrate-N
	--- μg g^{-1} oven dry soil ---	
Taheke ex-pasture	0.81 (0.71 - 0.82)	20.3 (16.4 - 27.8)
Taheke Pasture Site 1	0.81	40.9
Taheke Pasture Site 2	0.75	7.5
Whakarewarewa Forest	0.84	0.0

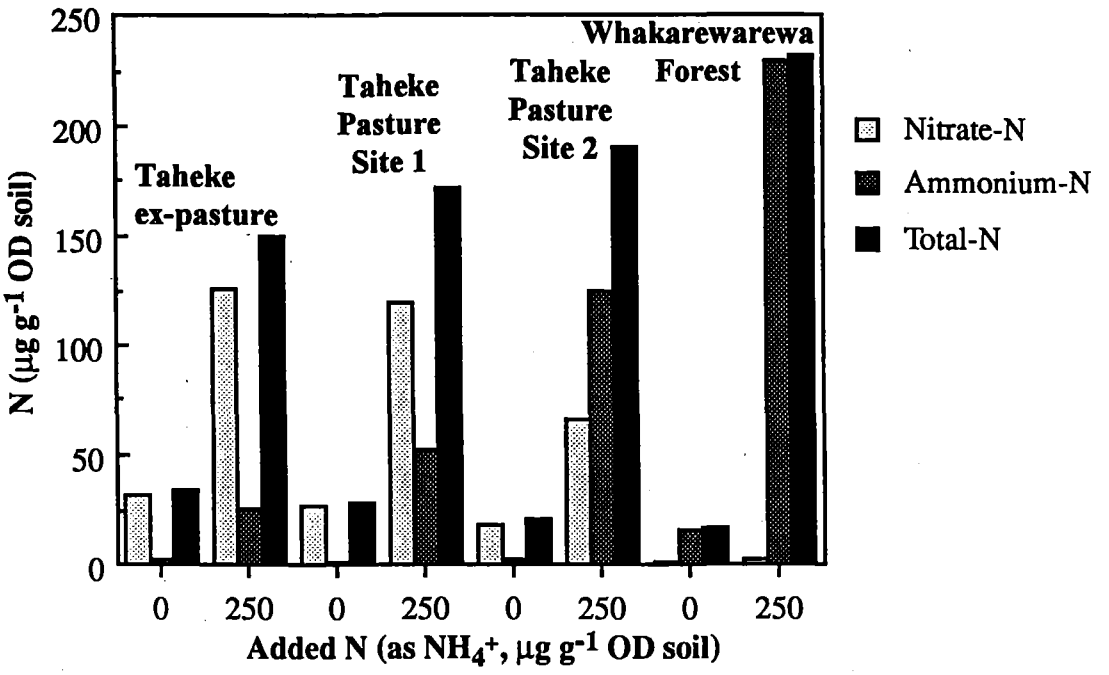


Figure 3.9: Effect of ammonium sulphate addition on the production of nitrate, ammonium and total N in an aerobic incubation of soil samples (0 to 10cm depth) from the Taheke ex-pasture and pasture sites and the Whakarewarewa Forest site.

For Taheke pasture site 2, nitrate-N was the dominant form of N in the control samples. With amendment both nitrate and ammonium N increased but ammonium production dominated representing 66% of the total N measured.

In the Whakarewarewa Forest samples, ammonium-N was present at high levels and represented 90% of the total N in the control samples and 99% in the amended samples.

The amount of N immobilised[2] by the amended samples in the aerobic incubation ranged from 112 to 155μg g^{-1}, in the Taheke ex-pasture samples, with a mean of 134μg g^{-1}. At Taheke pasture sites 1 and 2 and Whakarewarewa Forest the amount of N immobilised was 107, 81, and 36μg g^{-1} respectively.

3.3.5.2 Anaerobic incubation and total N

The amount of mineral N (**Table 3.6a**) and total N (**Table 3.6b**) in the Taheke ex-pasture samples in February and the changes in these factors since August were not significantly affected by the addition of N. The coefficients of variation were high and the control plots also showed similar gains in total N and losses of mineral N experienced by the fertilised plots (data not shown). At the

[2] Immobilised N was the amount of N unaccounted for from the 250μg g^{-1} added in the $(NH_4)_2SO_4$ amended samples:

$$250-((\text{Amended } NO_3^-\text{-N} + NH_4^+\text{-N}) - (\text{Control } NO_3^-\text{-N} + NH_4^+\text{-N}))$$

assuming no denitrification or volatilisation losses.

Taheke ex-pasture site, soil sampling date was significant for amount of mineral N in the 0 to 10cm ($p<.001$) and 10 to 20cm ($p<.001$) depths and for total N% ($p=.002$ and .021 respectively). While mineral N levels declined from August to February at both depths total N% increased.

The amounts of mineral N and total N in the Taheke pasture sites were similar to those of the Taheke ex-pasture site. For Whakarewarewa Forest the total N% at both soil depths was lower than the other sites while mineral N was only less than the other sites in the 0-10cm depths in August.

3.3.6 Correlations between soil N and tree growth characteristics

At the Taheke ex-pasture site in August, the levels of mineral N and total N% were significantly and negatively correlated with the amount of stem deformity, the number of kinks, height and DBH (**Table 3.7a**). As mineral N and total N% increased, tree growth and stem deformity decreased.

The changes in tree height from August to February were significantly and positively correlated with changes in soil mineral N at the 0 to 10cm and 0 to 20cm depths. Between August and February, changes in mineral N were negative (i.e. the amounts declined, see **Table 3.6a**) while the changes in tree height were positive. The correlations between these two factors indicated that the smaller negative changes in mineral N were associated with greater positive changes in tree height. The change in DBH was significantly and negatively correlated with mineral N (0 to 10cm) and positively correlated with mineral N (10 to 20cm) and total N% (0 to 20cm).

Table 3.6: Amount of a) mineral N, determined by anaerobic incubation, and b) total N in the soil cores from 2 depths at four sites in August 1989 and February 1990. The Taheke ex-pasture results are means from 12 plots (ranges in brackets). For Taheke Pasture site 1, there were no measurements for mineral N in February or total N%.

	August:		**February:**	
Site	0-10 cm	10-20cm	0-10cm	10-20cm
a)		--- $\mu g\ g^{-1}$ ---		
Taheke ex-pasture	148 (131 - 171)	45 (37 - 60)	96 (73 - 117)	27 (17 - 41)
Taheke Pasture Site 1	141	28	-	-
Taheke Pasture Site 2	116	45	83	23
Whakarewarewa Forest	77	60	87	36
b)		--- % ---		
Taheke ex-pasture	0.51 (0.44 - 0.58)	0.30 (0.26 - 0.38)	0.58 (0.51 - 0.67)	0.35 (0.27 - 0.42)
Taheke Pasture Site 2	0.46	0.25	0.52	0.31
Whakarewarewa Forest	0.20	0.17	0.29	0.20

Tree heights in February were significantly and negatively correlated with total N% in the 0 to 20cm and at 0 to 20cm depths. Tree DBH was also negatively correlated with total N% at 10 to 20cm and positively correlated with mineral N at 10 to 20cm.

In February, the levels of stem deformity and the number of kinks were significantly and positively correlated with total N% and mineral N. In contrast to August, the amount of stem deformity increased as total and mineral N increased.

There were significant correlations between tree form and incubation data. In February, increasing nitrate production by the control samples and increasing amounts of immobilised N in the amended samples significantly correlated with increasing stem deformity and number of kinks (**Table 3.7b**). Both stem deformity and the number of kinks were significantly and negatively correlated with nitrate production by the amended samples in the aerobic incubation.

3.3.7 Soil profiles

The soil profile descriptions from the Taheke ex-pasture and pasture sites and the Whakarewarewa Forest site (**Table 3.8**) were similar to those described for the area by Rijkse (1979). At the Taheke ex-pasture site, the correspondence of the horizons of the two profiles was very clear cut (J.A. Adams, pers. comm., 1989). The change in soil colour down both of the Taheke ex-pasture profiles suggested that there was a series of buried soils. This visual evidence was supported by the chemical analysis of the horizons (**Table 3.9**) as there were increases in all of the nutrients at depth.

From the surface, the first buried soil occurred at 46 and 35cm in Profiles 1 and 2 respectively and represented the next two horizons to a depth of 71 and 75cm (**Tables 3.8a and 3.8b**) However, this first buried soil was not chemically 'visible' as there was no increase in any soil nutrient levels (**Tables 3.9a and 3.9b**).

The second indication of a buried soil occurred at 71 and 75cm depth, in the Taheke ex-pasture Profiles 1 and 2 respectively, to a depth of 90cm. This was indicated by a change in soil colour and texture, from the buried soil above, and there were increases in the amount of organic C%, total N% and Bray 2 cations - particularly Bray 2 K in Profile 1 and Bray 2 Ca and Mg in Profile 2.

A third buried soil occurred at 90cm depth in both Taheke ex-pasture profiles. The amount of Bray 2 Ca and Mg increased in Profile 1. Bray 2 extractable P increased at the base of both profiles.

In the Taheke pasture 2 profile, buried soils were also present (**Table 3.8c**). The amounts of soil nutrients were similar to those found at Taheke except for the much lower amounts of Bray 2 K (**Table 3.9c**). Within the pasture profile there was no organic C%, total N% or Bray 2 K found in the 57 to 87cm horizon. Below this there was a buried soil indicated by a change in soil texture and also an increase in organic C%, total N% and Bray 2 cations compared to the horizon above.

At Whakarewarewa Forest, the Haparangi sandy loams are, like many of the composite yellow-brown pumice soils on yellow-brown loams, derived from weakly weathered young tephra over moderately weathered, older compacted tephra (Rijkse 1979) implying the presence of buried soils which was also suggested in the identification of the soil horizons (**Table 3.8d**). While the amount of Bray 2 extractable P increased at a depth of 48 to 98cm and Bray 2 Mg at the base of the profile (98cm +) the amounts of soil nutrients steadily declined down this profile (**Table 3.9d**).

Table 3.7: Significant linear relationships between a) plot means of radiata pine physical measurements and soil N characteristics at the Taheke ex-pasture site (August 1989 and February 1990) and b) February measurements of stem deformity and aerobic incubation N.

a) Tree physical characteristic	Soil N characteristic	Regression coefficient (r)	Probability level
August:			
Height	Mineral N, 10-20 cm	-.47	.123
DBH	Mineral N, 10-20 cm	-.52	.085
Stem deformity	Mineral N, 0-10 cm	-.59	.043
	Mineral N, 0-20 cm[#]	-.53	.078
	Total N%, 0-10 cm	-.66	.021
	Total N%, 0-20 cm	-.48	.119
Number of kinks	Mineral N, 0-10 cm	-.65	.021
	Mineral N, 0-20 cm	-.65	.022
Change - Aug to Feb			
ΔHeight	ΔMineral N, 0-10 cm	.66	.019
	ΔMineral N, 0-20 cm	.73	.007
ΔDBH	ΔMineral N, 0-10cm	-.57	.055
	ΔMineral N, 10-20cm	.52	.083
	ΔTotal N%, 0-20 cm	.50	.096
February:			
Height	Total N%, 10-20 cm	-.64	.026
	Total N%, 0-20 cm	-.44	.150
DBH	Mineral N, 10-20 cm	.45	.143
	Total N%, 10-20 cm	-.55	.066
Stem deformity	Mineral N, 10-20 cm	.57	.051
	Total N%, 0-10 cm	.67	.016
Number of kinks	Total N%, 0-10 cm	.62	.033

b) Tree physical characteristic	Aerobic incubation N characteristic	Regression coefficient (r)	Probability level
Stem deformity	Nitrate - unamended	.57	.052
	Nitrate - amended	-.64	.024
	Immobilised N - amended	.78	.003
Number of kinks	Nitrate - unamended	.54	.071
	Nitrate - amended	-.52	.082
	Immobilised N - amended	.72	.009

[#] The sum of depths 0-10 cm and 10-20 cm.

Table 3.8: Soil profile descriptions from the Rotorua district taken in August, 1989.

a) Taheke ex-pasture site - Profile 1.

Horizon	Depth cm	Colour	Texture	Comments
Ah	0 - 24	10YR2/1 Black	sl	Weak, v. fine and fine nut, v. friable, few to many lapillae.
B_{21}	24 - 36	10YR3/3 Dk. brown	ls	V. friable to loose, single grain, many lapillae.
B_{22}	36 - 46	10YR3/6 Dk. Yellowish brown	ls	V. friable, single grain, abundant lapillae.
IIuA	46 - 54	10YR2/2 V. dk. brown.	ls to sl	V. friable, single grain, many lapillae.
IIuB	54 - 71	10YR4/4 Dk. yellowish brown	ls	Loose, single grain, abundant lapillae.
IIIuB	71 - 90	10YR4/6 Dk. yellowish brown	sl	V. weakly devel., medium nut, greasy, few lapillae.
IVuB	90 - 115	10YR5/6 Yellowish brown	sl	V. weakly devel., fine nut, no lapillae.
IVuB	115 +	10YR6/8 Brownish yellow	ls	Single grain, v. friable, few lapillae.

b) Taheke ex-pasture site - Profile 2

Horizon	Depth cm	Colour	Texture	Comments
Ah	0 - 25	10YR2/1 Black	sl	Weakly devel, med. to fine nut, v. friable, few lapillae.
B	25 - 35	10YR3/3 Dk. brown	ls	Loose, single grain, many lapillae.
IIuB	35 - 45	10YR4/6 Dk. yellowish brown	sl	Loose, single grain, few lapillae (fewer than above).
IIuB	45 - 75	10YR3/3 Dk. brown	ls	V. friable to loose, single grain, many lapillae.
IIIuB	75 - 90	10YR3/6 Dk. yellowish brown	sl	V. weakly devel., friable, greasy, medium to fine nut, few lapillae.
IVuB	90 - 130	10YR5/6 Yellowish brown	sl	V. weakly devel., v. friable, greasy, fine nut, no lapillae.
IVuB	130 +	10YR6/8 Brownish yellow	ls	Single grain, v. friable, few lapillae.

3.8 c) Taheke Pasture Site 2

Horizon	Depth cm	Colour	Texture	Comments
Ah	0 - 28	10YR2/1 Black	sl	Weakly devel., med. nut and crumb (2-5mm), v. friable, few lapillae.
	28 - 57	10YR3/2 Brownish black	ls	V. friable, single grain, many lapillae.
	57 - 87	10YR6/6 Yellowish brown	sand	Loose, single grain, abundant lapillae.
IIuA	87 - 93	10YR4/2 Greyish yellow brown	sl	V. friable, many lapillae.
	93 - 110	10YR3/6 Yellowish brown	sl	V. friable, medium nut, few lapillae.
	110 +	10YR6/8 Yellowish brown	sl	V. friable, fine and med. nut (loose), abundant fine lapillae.

d) Whakarewarewa Forest

Horizon	Depth cm	Colour	Texture	Comments
L	2 - 5			
H	0 - 2	7.5R3/2 Dk. reddish brown		Distinct boundary
A_1*	0 - 13	10YR2/1 Black	sl	Weakly devel, fine and med. nut, v. friable, few lapillae, indistinct boundary.
(B)*	13 - 28	10YR3/6 Yellowish brown	ls	V. friable, weakly devel., med. nut, many lapillae, indistinct boundary.
II(B)*	28 - 48	10YR4/4 Brown	ls	V. friable, weakly devel., med. nut, mottled colours, few lapillae.
IIIu(B)*	48 - 98	10YR5/8 Yellowish brown	sl	Friable, weakly devel., med. nut, no lapillae.
	98 +	10YR4/6 Brown	ls	Friable, weakly devel., medium nut, few lapillae.

* Horizonation after Rijkse (1979).

Table 3.9: Soil nutrient data from the soil samples taken from the horizons of two profiles at the Taheke ex-pasture site, one profile at Taheke Pasture Site 2 and one profile in the Whakarewarewa Forest in August 1989.

a) Taheke ex-pasture site - Profile 1.

Depth (cm)	pH	Organic C%	Total N%	Bray 2 extractable P --- µg g^{-1} ---			Bray 2 cations --- me% ---		
				Ext.1	Ext. 2	Ext. 3	K	Ca	Mg
0-24	5.4	4.9	0.45	98	90	68	0.46	6.6	0.99
24-36	5.3	2.8	0.26	38	47	36	0.09	2.5	0.29
36-46	5.3	1.7	0.17	30	25	16.2	0.05	0.71	0.16
46-54	5.2	1.8	0.15	12.5	19.8	13.2	0.15	0.37	0.10
54-71	5.1	1.3	0.09	11.9	12.0	8.3	0.13	0.27	0.06
71-90	5.0	2.0	0.15	2.8	6.1	8.9	0.43	0.45	0.08
90-115	5.6	1.4	0.11	2.1	3.1	3.5	0.30	0.88	0.21
115+	5.8	0.4	0.01	4.2	8.7	14.2	0.10	0.62	0.11

b) Taheke ex-pasture site - Profile 2.

Depth (cm)	pH	Organic C%	Total N%	Bray 2 extractable P --- µg g^{-1} ---			Bray 2 cations --- me% ---		
				Ext.1	Ext. 2	Ext. 3	K	Ca	Mg
0-25	5.5	4.8	0.39	89	78	55	0.53	4.4	0.77
25-35	5.4	2.3	0.21	8.7	19.7	23	0.20	0.96	0.15
35-45	5.4	1.6	0.16	5.8	12.8	15.5	0.13	0.55	0.11
45-75	5.6	1.5	0.15	5.6	9.4	7.7	0.10	0.53	0.11
75-90	5.7	2.7	0.25	1.6	3.1	5.3	0.18	1.37	0.41
90-130	5.9	1.4	0.11	1.7	3.2	4.9	0.15	1.13	0.32
130+	6.1	0.4	0.02	5.1	12.1	22.5	0.05	0.58	0.27

c) Taheke Pasture Site 2

Depth (cm)	pH	Organic C%	Total N%	Bray 2 extractable P --- µg g^{-1} ---			Bray 2 cations --- me% ---		
				Ext.1	Ext. 2	Ext. 3	K	Ca	Mg
0-28	5.7	5.5	0.41	61	54	42	0.04	4.0	1.20
28-57	6.0	1.2	0.10	121	27	9.7	0.00	0.85	0.11
57-87	6.6	0.0	0.00	24	6.5	4.0	0.00	0.25	0.05
87-93	6.0	2.3	0.12	5.3	5.0	3.5	0.05	1.83	0.28
93-110	6.0	1.6	0.16	2.3	5.1	8.5	0.06	1.73	0.27
110+	6.0	0.8	0.07	4.8	9.1	17.9	0.05	0.75	0.14

3.9 d) Whakarewarewa Forest

Depth (cm)	pH	Organic C%	Total N%	Bray 2 extractable P — μg g^{-1} —			Bray 2 cations — me% —		
				Ext.1	Ext. 2	Ext. 3	K	Ca	Mg
0-13	5.6	3.9	0.27	13.5	11.2	9.0	0.09	4.2	0.95
13-28	5.9	3.2	0.17	11.0	29	24	0.03	2.0	0.43
28-48	6.0	2.4	0.14	3.1	9.0	19.8	0.03	0.70	0.17
48-98	5.8	1.0	0.06	5.2	9.6	16.5	0.01	0.33	0.11
98+	5.8	0.6	0.03	2.2	4.0	5.2	0.03	0.22	0.15

Compared to the Taheke ex-pasture profiles and the Taheke pasture site 2 profile, the most obvious difference at Whakarewarewa Forest was the amount of Bray 2 extractable P which was much lower particularly in the surface horizons **(Table 3.9d)**.

In all four profiles the pH levels were in the 5.0 to 6.1 range.

3.4 DISCUSSION

3.4.1 Soil Analysis

The soil profiles sampled at Rotorua were all deep and there was evidence of buried horizons in the descriptions of the Taheke ex-pasture profiles and the Taheke pasture site 2 profile. This was supported by the amounts of soil nutrients whose increases at depth coincided with visual and textural changes in the soil horizonation associated with the presence of a buried soil. Changes occurred for organic C%, total N%, Bray 2 extractable P and Bray 2 cations and the presence of a buried soil was usually indicated by an increase in one or more of these soil nutrient measurements. According to Rijkse (1979) the Whakarewarewa Forest soil also contained several buried soils but this was not obvious from the chemical data whose levels tended to decrease with depth.

The soil profiles sampled could be described as "multisequal" as they contain repetitions of soil horizons associated with buried soils (Tonkin *et al.* 1992) as a result of the continued addition of volcanic parent material. Even within the Taheke ex-pasture site there were differences in the horizonation and nutrient contents of the two soil profiles which were approximately 35m apart. The Taheke ex-pasture profile 2 did not have a IIuA horizon at a depth of 45 to 55cm and there were differences in the concentrations of Bray 2 extractable P and Bray 2 cations particularly at depth.

In multisequal soils features such as the amount of nutrient present in the parent material, soil nutrient exchange and retention capacity and the amount of weathering that occurs before and after further volcanic additions can vary from horizon to horizon. Knight and Will (1970) found that the amounts of total N and P and exchangeable Mg and K differed markedly between layers in a pumice soil profile at Kaingaroa Forest.

Thus the depth of these multisequal profiles and the variable thicknesses of the horizons within them adds to the difficulty of correlating soil nutrient parameters with the foliar nutrient concentrations of radiata pine whose root system is capable of exploiting a large volume of these very friable and well-drained soils.

According to the ratings for chemical properties used by the Soil Bureau for New Zealand soils (Blakemore *et al.* 1987) the topsoils (0 to 25 cm) of the Taheke ex-pasture profiles and the Taheke pasture site 2 profile were moderately acid (pH 5.3 to 5.9) and slightly acid (6.0 to 6.5) respectively and rated medium for the amounts of organic C% (4 to 10%) and total N% (0.3 to 0.6%). The amounts of cations extracted by the Bray 2 method are comparable to the cation concentrations found by ammonium acetate leachings (Ballard 1978) thus, according to Blakemore *et al.* (1987) the Bray 2 K levels were very low (<0.3 me%) in the Taheke pasture site 2 profile and low (0.3 to 0.5 me%) to medium (0.5 to 0.8 me%) in the Taheke ex-pasture profiles. Bray 2 Ca was low (2 to 5 me%) to medium (5 to 10 me%) and Bray 2 Mg was low (0.5 to 1.0 me%) in the Taheke ex-pasture profiles and medium (1 to 3 me%) in the Taheke pasture site 2 profile.

The Whakarewarewa Forest profile was moderately acid, organic C% and total N% were low (2 to 4% and 0.1 to 0.3% respectively), Bray 2 K was very low and Bray 2 Ca and Mg (0.1 to 0.3%) were low. Generally this profile rated lower for the levels of C, N and Mg compared to the Taheke ex-pasture profiles. There were also differences in Bray 2 extractable P and the nitrification pathway. The concentrations of Bray 2 P extracted from the surface soils of the Taheke ex-pasture and Taheke pasture site 2 profiles were much higher than that extracted from the Whakarewarewa Forest profile. According to Skinner *et al.* (1991) the Taheke ex-pasture and Taheke pasture site 2 profiles would rate as Category 4 where "Bray P concentrations in the first extraction are markedly in excess of 12μg P g^{-1} soil, and ... 'available' P declines slowly with successive extractions". The results from fertiliser trials in conventional forests presented by Skinner *et al.* (1991) indicated that the first extraction of the Category 4 soil would result in a Bray 2 extractable P concentration of 24 to 31 μg g^{-1}. At the Taheke ex-pasture site, the concentration of Bray 2 extractable P was much higher in the first extraction, at 88.6 and 98.3μg g^{-1} in the top 25cm, and the third Bray 2 extractable P sequential extractions were yielding in excess of 12μg g^{-1} of P down to about 45cm. In contrast, in the Taheke pasture profile Bray 2 extractable P levels were highest at 120.5μg g^{-1} in the first extraction, at a depth of 28 to 57 cm, but declined rapidly compared to the sequential extraction of the 0 to 28 cm horizon. Clearly these ex-improved pasture soils in the Taheke area are outside the bounds of conventional forest experience in New Zealand and highlight the level of P accumulation that has occurred as a result of fertiliser additions to these agricultural soils.

At Whakarewarewa Forest, a mature conventional forest system, the sequential extraction of Bray 2 extractable P from the soil at a depth of 0 to 13cm was almost a combination of Categories 3 and 4. While the initial extraction results in Bray 2 extractable P concentrations only just in excess of 12 μg g^{-1}, the decline of Bray 2 extractable P with successive extractions was not rapid as is the criteria for a Category 3 soil. In contrast, the next horizon, at a depth of 13 to 28 cm, showed an increase in Bray 2 extractable P concentrations with sequential extraction from 11.0 to 23.6 μg g^{-1}. This trend was reflected in the horizons below, although the amounts of Bray 2 P extracted were declining, and also occurred in the Taheke ex-pasture and pasture site 2 soil profiles at various depths. The implications of these results in relation to the availability of P for radiata pine is discussed later.

As hypothesised, the nitrification pathway also differed between the Taheke ex-pasture and pasture soils and Whakarewarewa Forest soils at a depth of 0 to 10cm. In the unamended incubations (i.e. 0 Nμg g^{-1} soil) nitrate was the dominant form of inorganic N in the Taheke ex-pasture and pasture

samples and ammonium in the Whakarewarewa Forest samples. In the incubated soils from the Taheke ex-pasture and pasture sites autotrophic nitrification occurred as nitrate levels were promoted by the addition of ammonium-N and the concentration of ammonium decreased from the original 250μg g^{-1} added to the samples. At Taheke pasture site 2, nitrate-N concentrations did increase from 18.7 to 65.4 μg g^{-1} - but the remaining ammonium was the dominant form of N. The differences between the two Taheke pasture profiles may have been related to differences in soil conditions which affected the nitrifying microbial populations.

In the Whakarewarewa Forest 0 to 10cm soil samples the added ammonium was not converted to nitrate-N but nitrification did occur at similar, although very low, levels in the control and amended samples. As ammonium addition did not promote nitrate levels, the results suggest that there may have been a low amount of nitrification via an autotrophic and/or heterotrophic pathway. As the time of the aerobic incubation was relatively short, the population of autotrophic nitrifiers may not have had time to build up in response to the ammonium additions (J.A. Adams, pers. comm., 1993). For instance, Birk (1991) used nineteen week laboratory incubations to determine nitrification potentials in forest soils. The presence of a heterotrophic pathway at Whakarewarewa Forest would have to be confirmed using organic-N amendment as described by Adams (1986).

As the pH values in the 0 to 10cm depths were similar for all sites (5.4 to 5.7), pH could not be used as a criterion to predict the likely nitrification pathway. Theodorou (1984) found that nitrification rates under pasture were greater than those under pine and stated that this was probably due to the differences in root biomass which was 4 times greater in the pasture than in the soil. The greater pasture root biomass can exude more energy sources for microbial growth and with a more uniform distribution compared to trees (Bowen 1973). Therefore, it appears that characteristics other than pH determined the respective nitrification pathways at the two sites by encouraging or inhibiting certain nitrifying microbial populations.

For the Taheke pasture site 1 and 2 samples, and especially the Taheke ex-pasture samples, a significant proportion of the 250 μg NH_4+-N g^{-1} added was unrecovered - 43, 32 and 53% respectively. Immobilisation in an increasing population of autotrophic nitrifiers, or other soil microbes encouraged by the optimal moisture and temperature conditions, was the most probable fate of the unrecovered N. Other possible fates for the added N were denitrification and volatilisation. Biological denitrification occurs in anaerobic conditions while volatilisation losses are highest when the soil pH is high (McLaren and Cameron 1990). As the incubation samples of the soils were not saturated and the soil pH was moderately to slightly acid, the possibility of the loss of the added N via denitrification or volatilisation was considered to be insignificant.

In the Whakarewarewa Forest amended samples, only 14% of the added N was unaccounted for. Immobilisation of the added N was minimal suggesting that the population of microbes did not respond to N addition. There was a significant (p=.024) correlation between nitrate production and the amount of N immobilised by the amended soil samples. The greater the amount of immobilisation the greater the amount of nitrate production (**Figure 3.10**) possibly reflecting a larger, more responsive microbial population particularly in the Taheke ex-pasture and pasture site 1 soils.

The implications of the aerobic incubation results were that urea and ammonium-based N fertilisers, when added to the soils in the Taheke ex-pasture site, would, amongst other fates, be converted to nitrate.

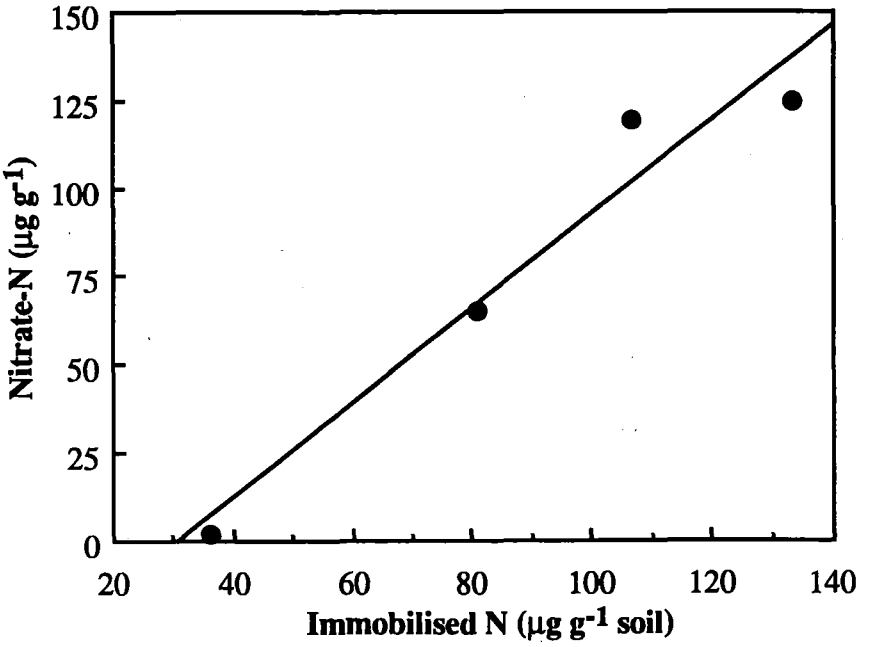


Figure 3.10: Correlation between the amount of N immobilised and nitrate production in ammonium amended soil samples during an aerobic incubation (p=.027).

The amount of mineral N in the core samples from the Taheke ex-pasture and pasture sites was higher than at Whakarewarewa Forest particularly in August in the 0 to 10 cm depth. N mineralised during incubation was always significantly greater in pasture soils than pine soil according to Theodorou (1984). This could reflect higher N totals available in the pasture soils and a more numerous and active microbial population. However by February mineral N levels were similar at the two sites as the amount of mineral N, in the core samples, decreased from August to February at the Taheke ex-pasture and pasture sites (both depths) and increased at Whakarewarewa Forest in the 0 to 10cm depth. A reduction in mineral N at the Taheke ex-pasture site and the Taheke pasture site 2 may reflect increased plant and soil microbial uptake during the spring and summer and generally a greater demand on soil N by the pasture and/or trees. For instance, Clinton (1990) found that the removal of N from the soil by the pasture in an agroforest system was highest in September.

There was a large difference in the soil total N% of the Taheke ex-pasture and pasture sites and the Whakarewarewa Forest site which may be related to their land use histories and the use of legumes and/or inorganic N fertilisers during pasture development and maintenance. The amount of total N% increased from August to February at all sites and for both depths. The increase was most likely a result of the return of N to the soil via plant litter inputs. At the Taheke ex-pasture site the changes in total N% were not a result of the N fertiliser addition which did not significantly affect the amount of total N% or mineral N in the soil. Knight *et al.* (1983) also found that the application of 168kg N ha^{-1} had no obvious effect on the status of soil total N. They attributed this to a large "background" level of soil N compared to the amount of N added, small-scale heterogeneity for total N within the plots and the rapid movement of the added N from the forest floor.

3.4.2 Tree response

3.4.2.1 Nutrient concentrations in the control plots

From October to February at the Taheke ex-pasture site, the factor of sampling date explained more of the variation in nutrient concentrations in the radiata pine foliage than the effect of N addition. There were no universal trends for the changes in nutrient concentrations with time (**Table 3.1**) but generally concentrations were higher in August and fluctuated to lower values in February.

Seasonal changes in the foliar concentrations of nutrients in radiata pine have been observed before (e.g Mead and Will 1976). Knight (1978) found that the fluctuations in foliar nutrient concentrations with time appeared to be related to tree demand, which is high during growth flushes; the internal mobility of nutrients, and microbial and root activity in the soil which is higher during the warmer summer months. In this study the nutrient concentrations tended to be lower during late summer when rainfall levels were also low (**Figure 3.2**). The warmer than normal temperatures (**Figure 3.3**) would have been conducive for tree growth providing other factors such as soil moisture and nutrient supply were not limiting. If, during drier periods, the trees were unable to take up adequate amounts of nutrients from the soil then retranslocation of mobile nutrients within the trees may have been an important mechanism. This would have reduced needle nutrient concentrations in order to provide for new foliage growth.

The significant correlation between Ca and Zn concentrations and the amount of rainfall in the month prior to foliage sampling in the control plots (i.e. July, September, November and January in **Figure 3.5**) was related to the rainfall pattern which peaked in October and then declined. This pattern matched the changes in Ca and particularly Zn concentrations. Those nutrients, such as P and B, whose concentrations have been reportedly linked to rainfall (Hill and Lambert 1981, Fife and Nambiar 1982, and Turner and Lambert 1986) did not exhibit this relationship at the Taheke ex-pasture site. As the foliar concentrations of both P and B were marginal in February, retranslocation may have been the major influence on their concentration changes with sampling date.

It should be noted that the significant correlation between rainfall and Ca and Zn foliar concentrations was based on 4 numbers in one growing season. Foliar concentrations usually fall during rapid tree growth in the spring (e.g. Knight *et al.* 1983). This did occur for a number of nutrients in October (**Table 3.1**) however the concentrations of both Zn and particularly Ca increased.

Thus at the Taheke ex-pasture site, the fluctuations in nutrient concentrations with sampling date may have been a result of reduced/increased nutrient uptake, which may have been affected by rainfall, and retranslocation of nutrients to/from the needle depending on the mobility of that nutrient.

The higher than normal summer temperatures measured at Rotorua Airport may also have had an important effect on foliar nutrient concentrations of the radiata pine trees growing on the Taheke ex-pasture site. Increased temperatures may increase tree growth and demand for nutrients, increase microbial and root activity in the soil and affect chemical processes in the soil related to nutrient supply. The relationship between temperature and foliar nutrient concentrations was not examined during the study described in this chapter.

3.4.2.2 Effect of adding N

The addition of N to the radiata pine growing at the Taheke ex-pasture site had a short-term affect on foliar N and Cu concentrations which significantly increased in October. The increase in N concentrations due to N fertiliser addition was proportionally small. In October the addition of 500kg N ha^{-1} raised foliar concentrations from the control 1.76% to 1.87%. The N% in the control was greater than 1.6% throughout the trial confirming that, as N addition only significantly increased N% in the short-term and the amount of total N% in the soil was medium, N was not a limiting nutrient at this site.

The addition of N significantly reduced the concentrations of P, Ca and Mg in December. Only the P concentrations were significantly less with added N in February.

The February concentrations of P, Mg and B were less than the satisfactory standard values of Will (1985). The marginal concentrations of P in the control plots were unexpected considering the high Bray 2 extractable P concentrations that were measured in the topsoil at the Taheke ex-pasture site. The Bray 2 extractable P results put this soil well in excess of the top Category 4 rating and yet foliar P concentrations were less than 0.14% - particularly where N fertilisers had been added. It should be noted that the Bray 2 extractable P Categories described by Skinner *et al.* (1991) were based on the analysis of soils from a depth of 0 to 10 cm. In an agroforest this is the site of competition for soil nutrients between the pasture and the trees. For instance, Clinton (1990) found that $^{15}NH_4$+ added to a radiata pine-pasture agroforest was rapidly immobilised in the pasture. The removal of this competition increased the uptake of ^{15}N by the radiata pine and the amount of KCl-extractable mineral-N from the soil.

As pasture roots can have a density of 30 to 50cm cm^{-3} in the top 10 cm of the soil (Barley 1970) compared to 3 to 4 year-old radiata pine at 0.15 and 0.31 cm cm^{-3} in the 0-10 and 10-20 cm depths respectively (Nambiar 1983) the trees may be encouraged to exploit lower soil depths in search of nutrients. In such a situation the Bray 2 extractable P categories of deeper soil depths may better reflect the availability of P to the trees. Below the topsoil there was variation in the concentrations and pattern of Bray 2 extractable P extracted sequentially (**Table 3.9a and 3.9b**) both within and between the two Taheke ex-pasture soil profiles. However, to a depth of at least 45cm the soils still appear to contain adequate levels of "available" P although there may be large variation in P soil status across the Taheke ex-pasture site given the differences between the two profiles sampled.

The Mg concentrations in February were marginal in the Taheke ex-pasture control plots and low, but not significantly different, where N had been added. These Mg concentrations could be expected as the soil analysis indicated that the amount of Bray 2 Mg was low in the topsoil (0 to 25cm) and very low in the horizons below 25cm.

Soil B at the Taheke ex-pasture site was measured with a fractionation scheme (Chapter 6) where the concentration of "non-specifically adsorbed" B was 1.0μg g^{-1} in the top 25cm. This concentration was three times the 0.33μg g^{-1} found in the control soil (0 to 10cm) at Ashley Forest which is considered a marginal site for radiata pine B nutrition. The availability of native soil B is partly a function of the parent material (J.A. Adams, Z. Hamzah and R.S. Swift, unpublished) and radiata pine B deficiencies can be associated with droughty coarse-textured soils (Hunter *et al.* 1990b) and soils of volcanic origins (Lambert and Turner 1977). Boron availability to the trees is governed by factors such as rainfall, soil depth, and moisture (Will 1985). During the trial the monthly rainfall was less than normal and, in the well-drained soils at the Taheke ex-pasture site, may have resulted in a reduction of B uptake from the soil.

The concentrations of Bray 2 Ca and K in the Taheke ex-pasture site topsoil were low to medium. In February the radiata pine foliar concentrations of Ca and K, at an average of 0.18 and 1.0%, were well in excess of the satisfactory standard values of 0.1 and 0.5% respectively.

It should be noted that the soil data are based on profile samples collected in August and are being compared with standard foliage nutrient values from the February sampling. It was assumed that the soil nutrient levels, other than mineral N, would not change significantly from August to February.

As previously described, the soils at Taheke and Whakarewarewa were fundamentally different in their land use histories which has consequently affected soil nutrient levels such as C% and Bray 2 Mg and particularly total N% and Bray 2 extractable P which were all lower at Whakarewarewa Forest.

The standard foliar nutrient values that have been designated 'low', 'marginal' and 'satisfactory' for radiata pine in New Zealand (Will 1985) have been identified through extensive trials in conventional forests on typically poorer soils than those found in agroforestry systems. The relevance of these standards to radiata pine growing in the different environmental circumstances provided by the agroforest has yet to be assessed.

Other foliar diagnostic techniques have been used to identify nutrient imbalances and the requirement for fertiliser additions for radiata pine. For instance ratios between Cu and N appear to have a greater diagnostic value than either Cu or N concentrations alone. Turvey (1984) stated that Cu:N ratios for radiata pine were a sensitive indicator of Cu fertiliser treatment. Van den Burg (1983) indicated that a high N level increased the critical Cu concentration and N:Cu ratios could therefore be useful in determining the critical Cu concentration.

At the Taheke ex-pasture site, increasing addition of N did not significantly affect Cu:N ratios (**Table 3.3**) except for the February results where the ratio significantly declined from 2.6 at N_0 to 2.3 at N_{250}. However, the Cu:N ratio at the highest N rate, N_{500}, was not significantly different from that at N_0 and N_{250}.

In February the Cu:N ratios were significantly and negatively correlated with the number of kinks measured in the leader growth since August (**Table 3.4**). This is discussed later in this chapter.

3.4.2.3 Tree physical growth

At the Taheke ex-pasture site, due to the height, branchiness and dense foliage of the radiata pine trees the actual physical measurement of the twists and kinks that constituted speed wobbles was not practicable. Therefore a visual assessment of the number of kinks, and their severity per tree, was made on the visible leader in August and on the leader growth, since August, in February.

The direct effect of adding 250 and 500kg of N ha^{-1} to the Taheke ex-pasture site was undetectable in radiata pine tree growth, even after 6 months. While the physical measurements of height, diameter and stem deformity increased from August to February, these changes could not be attributed to the addition of the N fertiliser. Such a lack of physical tree response to large N additions has been found before by Hopmans and Flinn (1991) where differences in radiata pine tree height, as a result of N fertilisation at 200 and 600kg ha^{-1} to 2 year-old trees, were negligible after three years on an improved legume pasture site. Mead *et al* (1984) found that N fertilisation significantly accelerated maximum canopy development and increased the fraction of dry matter

allocated to the crowns. This may also have occurred at the Taheke ex-pasture site where increasing N addition could have promoted crown growth rather than tree height and diameter which were the measurements taken.

The level of stem deformity has been found to increase with N fertiliser addition. Hopmans and Flinn (1991) investigated the effect of available soil N on 2 year-old radiata pine stem deformity on sites with contrasting land use histories of native forest, improved legume pasture and tobacco cropping. They found that the percentage of radiata pine, growing on an improved legume pasture, with serious growth deformities was high at 63%. The addition of 600kg N ha^{-1} significantly increased this to 73%. Proportionally, the fertiliser only had a small effect on stem deformity compared to the 'background' level already present at this site. A similar result was found for the ex-tobacco site where stem deformities affected 66% of the trees, without N addition, and this increased, but not significantly, to 72% with the addition of 600kg N ha^{-1}. The results of Hopmans and Flinn (1991) suggest that the addition of N has a much more substantial effect on sites of low to moderate fertility status. In their study this was represented by the native forest site. With no added N the % of trees with stem deformities was 11. This increased significantly to 22 and again to 48% with the addition of 200 and 600kg N ha^{-1} respectively.

The majority of trees at the Taheke ex-pasture site already exhibited some degree of stem deformity in August, prior to N addition (see **Figure 3.8**), which increased from August to February but not as a direct result of N addition. It seems likely that the N fertiliser was added to a system that already had a large N pool in the soil. Therefore the addition of 500kg N ha^{-1} did not represent a significant input into this system. Converting the Taheke ex-pasture soil total N% and mineral N data indicated that the total amount of soil N present in the 0 to 10 and 10 to 20cm depths in August were 3.1 and 1.8t ha^{-1} respectively (assuming a bulk density of 0.6g cm^{-3}, J. Adams, pers. comm., 1992). The proportion of potentially mineralisable N, from anaerobic incubation (**Table 3.6**), was 89 and 27 kg ha^{-1} respectively. Compared to the total amount of soil N that was already present, the N addition was small - even when only considering the top 20 cm - but compared to the amount of mineral N the addition appears to be large. However, there were a number of likely fates for the added N that may have prevented the added N from entering a pool that was immediately accessible to the tree. For instance, immobilisation by soil microbes, uptake by the pasture and incorporation on the soil exchange may have been the fate of the added N.

Volatilisation, denitrification and leaching were unlikely to occur at this site. Factors favouring volatilisation and denitrification are high soil pH and anaerobic conditions respectively - both conditions are not characteristic of the Taheke ex-pasture site. Leaching was also an unlikely fate of the added N. Although the rainfall in October was high (**Figure 3.3**) the volcanic soils have a high water holding capacity. After October the rainfall was relatively low. In summer the low rainfall may have reduced soil moisture levels and nutrient supply to the tree via the soil solution. Cameron (1988) described agroforestry (eucalypts and pasture) research in SE Queensland and found that "even in this relatively equable climate" the major controlling factor for tree and pasture growth was the availability of soil water.

It is possible that the effect of the N addition was short-term, as shown in the foliar nutrient concentrations of N%, and that the pulse of N addition was soon masked by the high background amounts of soil N at the Taheke ex-pasture site.

As N addition was not instrumental in increasing radiata pine stem deformity at the Taheke ex-pasture site, some other factor(s) must have been the cause. Further investigation indicated that from August to February plots 1 to 7 had large increases in the average amount of stem deformity per plot while plots 8 to 12 had proportionally smaller and similar increases in stem deformity (**Figure 3.11**). These results indicated that there may have been some important site differences, possibly related to the soil characteristics of the trial site, that may have been causing the stem deformities - assuming there was no significant tree genetic variation or climate gradient across the site. For instance, 'plot' was highly significant for the differences in the number of kinks (p=.001) and stem deformity (p=.066) in February and height (p=.034) and DBH (p=.063) in August (**Table 3.10**). There were also significant (p<.05) plot differences for February heights and DBH's and the % change (%Δ) in these measurements from August to February. 'Plot' was not significant for the actual change in height or DBH from August to February. Considering the differences in the average plot physical tree measurements shown in **Table 3.10** - certain plots from numbers 1 to 5 had significantly higher August and February heights and diameters and, in February, significantly greater stem deformity and numbers of kinks than certain plots from 6 to 12. The % change in these measurements from August to February were more evenly distributed and tended to be greater in plots 6 to 12.

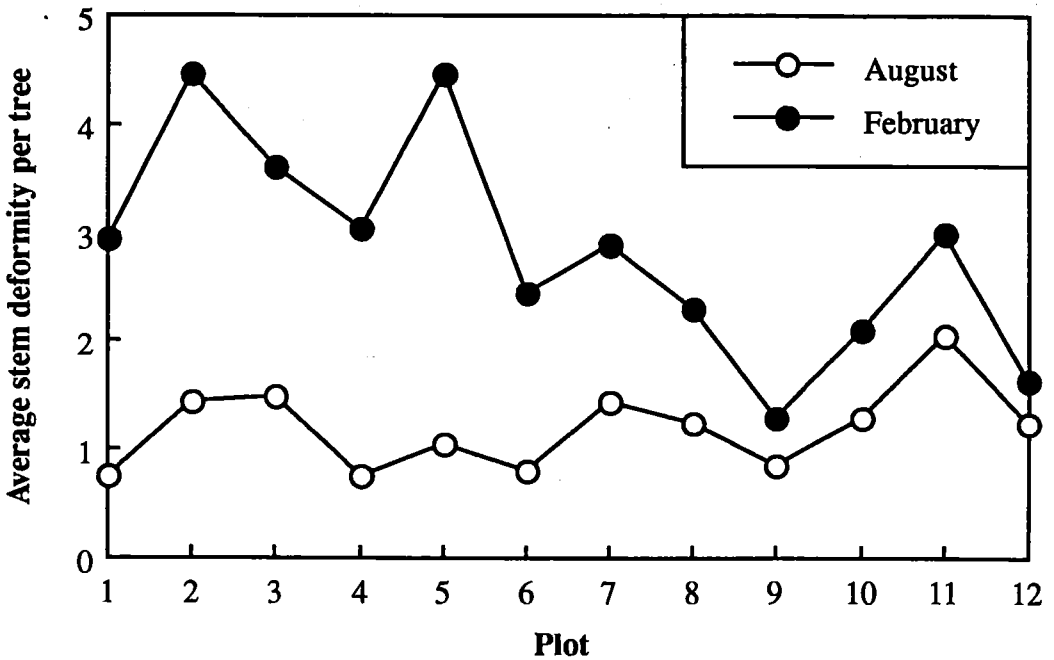


Figure 3.11: Average stem deformity per radiata pine tree in August 1989 and February 1990 in each plot of the Taheke ex-pasture site.

Closer inspection of the trial layout (**Figure 3.12**) showed that plots 1 to 5 were at the base of a steep slope. This area of the trial site may have promoted tree growth through higher levels of soil moisture, from water drainage down the slope, and thus encouraged greater water and nutrient uptake by the trees especially during the drier than normal summer. Other factors that may be involved include temperature gradient across the trial site and the shelter of some areas of the trial site from prevailing winds.

Table 3.10: Effect of plot number on radiata pine tree physical measurements and the probability of a plot main effect (p) at the Taheke ex-pasture site. For each physical measurement in each month, means with the same letter were not significantly different ($p<.05$).

		1	2	3	4	5	6	7	8	9	10	11	12	p
Stem deformity	Feb	3.0 abc	4.5 a	3.6 ab	3.1 abc	4.5 a	2.5 abc	2.9 abc	2.3 bc	1.5 c	2.1 bc	3.0 abc	1.7 bc	.066
No. of kinks	Feb	1.8 bcd	2.3 abc	2.7 ab	1.9 bcd	3.1 a	1.7 cd	1.8 bcd	1.8 bcd	1.0 d	1.9 bcd	1.7 cd	1.4 cd	.001
Height	Aug	4.2 a	4.2 a	4.2 a	3.8 ab	3.7 ab	3.6 b	3.6 b	3.9 ab	3.7 ab	4.0 ab	3.5 b	3.6 b	.034
	Feb	5.6 ab	5.8 a	5.6 ab	5.3 ab	5.2 ab	5.0 b	5.1 b	5.4 ab	5.1 ab	5.5 ab	5.0 b	5.0 b	.165
%ΔHt		36 ab	37 ab	32 b	40 ab	44 a	40 ab	44 a	40 ab	36 ab	39 ab	43 a	38 ab	.291
Diameter	Aug	8.0 ab	8.8 a	8.3 ab	7.3 abc	7.3 bc	7.0 bc	7.0 bc	7.1 bc	7.3 bc	7.3 bc	6.0 c	7.0 bc	.063
	Feb	11.6 ab	12.5 a	12.0 ab	11.0 abc	11.0 abc	10.9 abc	10.7 bc	10.5 abc	10.9 abc	10.8 abc	9.7 c	10.6 bc	.153
%ΔDBH		48 bc	43 c	47 bc	52 abc	54 abc	60 ab	57 abc	50 bc	54 abc	50 abc	65 a	53 abc	.234

3.4.2.4 Correlations between foliar and soil nutrient levels and tree physical growth

Because site factors appeared to be having the greatest effect on tree growth during the trial, correlations were made between the trees physical appearance (plot means for stem deformity, number of kinks per tree and tree height) and foliar nutrient concentrations and ratios and soil nitrogen characteristics in an attempt to identify those factors involved in the development and alteration of tree growth.

In August, height was the only measurement of tree growth that correlated with foliar nutrient concentrations and nutrient:N ratios. As the concentrations of N, P and Zn increased so did tree height - these correlations were significant particularly for P and Zn. The higher levels of these nutrients in the foliage possibly corresponded to a greater nutrient availability in plots 1 to 4. If the amount of nutrients in the soil profiles at the Taheke ex-pasture site were an indication of nutrient levels across the site (**Figure 3.12**) then greater amounts of N, P, Ca and Mg (**Table 3.9**) were available in plots 1 to 4 than plots 7 to 10. The amount of 'available' Zn was similar in both profiles (see Chapter 6).

In February, as the foliar concentrations of N and Zn increased so did the mean level of stem deformity. As neither N nor Zn showed any negative correlations with other foliar nutrients, the effect was probably not one of antagonism between nutrient concentrations. However, it should be noted that the measurement of foliar nutrient concentrations does not necessarily reflect the proportion of nutrient utilised by the trees' metabolic processes.

Hopmans and Flinn (1991) noted that stem deformities on fertile sites were not generally associated with a specific nutrient deficiency and this was the case at the Taheke ex-pasture site where stem deformity appeared to be associated with increases in nutrient concentrations rather than with nutrients that were at less than satisfactory levels. However the high concentrations of foliar N may have resulted in imbalances between N and other nutrients. This hypothesis was tested by examining the relationship between nutrient:N ratios and plot means for physical tree growth measurements (**Table 3.4**). For August heights there were significant and positive correlations between P:N and Zn:N ratios - as P and Zn concentrations increased relative to N, tree heights increased. The correlations between Ca:N and Mg:N and August tree heights was negative - as Ca and Mg concentrations increased relative to N, tree heights decreased. Higher Ca:N and Mg:N ratios were associated with plots 7 to 12.

Of particular interest was the significant correlation between Cu:N ratios and stem deformity in February - as Cu concentrations increased relative to N, the number of kinks per tree decreased (**Table 3.4**). The relationship between low Cu:N and higher numbers of kinks indicated a possible imbalance between Cu and N which may make the new leader vulnerable to deformation (kinking). The severity of the deformity may be related to the trees exposure to mechanical factors such as wind and rain as suggested by Will (1986). Due to the undulating terrain at the Taheke ex-pasture site, some plots may have been more exposed to the effect of wind than others. However, Hopmans (1990) found that Cu:N ratios were similar in the foliage of straight and deformed radiata pine.

At the Taheke ex-pasture site, the Cu:N ratios ranged from 1.8 to 3.1 in February. The values for Cu:N ratios from Hopmans (1990) ranged from 3.1 to 4.1 and were higher than those found at the Taheke ex-pasture site where Cu concentrations in the foliage were lower. Turvey (1984) found a lower critical Cu concentration in radiata pine of 3 to 4$\mu g\ g^{-1}$. Concentrations of Cu below this were associated with Cu:N ratios less than 1.3. The Cu:N ratios at the Taheke ex-pasture site exceeded this.

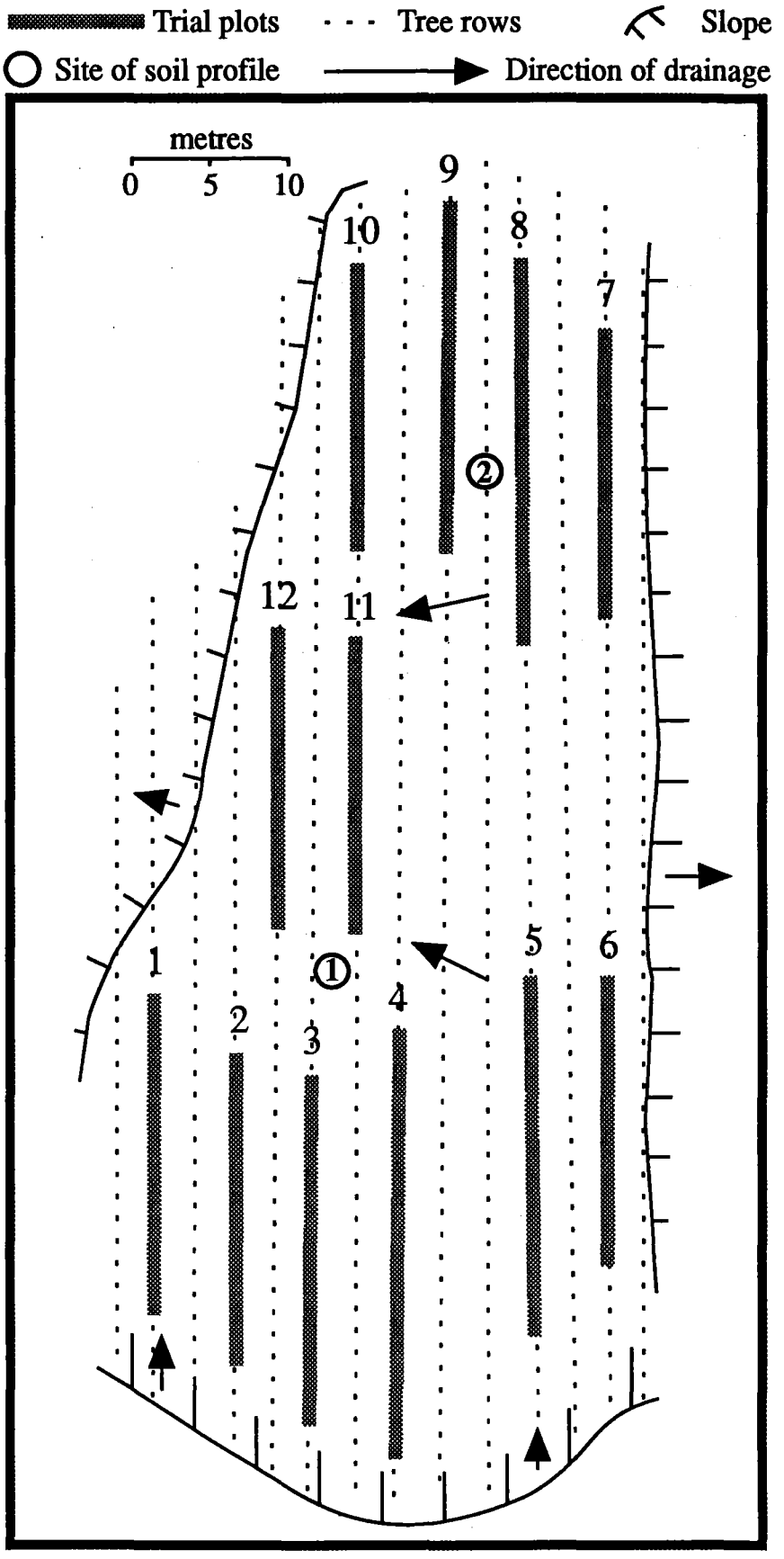


Figure 3.12: Trial layout at the Taheke ex-pasture site showing plot positions and drainage patterns.

At the Taheke ex-pasture site, as the foliar Cu concentrations did not significantly correlate with stem deformity measurements, it appears that Cu:N ratios may be of diagnostic value in determining the relationship between Cu and N and its possible effect on stem deformity.

In August all of the significant correlations between measurements of stem deformity and soil mineral N and/or soil total N (**Table 3.7a**) were negative. Thus higher amounts of mineral N and total N% were associated with trees of smaller height and DBH and less stem deformity. In February, tree growth showed a similar response - generally smaller trees were associated with high levels of total N%, at 10 to 20cm depths particularly, but increased stem deformity was associated with increases in total N% (0 to 10cm) and mineral N (10 to 20cm). There appeared to be differences in the effect of the two soil depths on tree growth. An example was the change in DBH, from August to February, being negatively correlated with changes in mineral N at 0 to 10cm but positively correlated with changes in mineral N at 10 to 20cm depths. These differences may be related to the abundance of tree roots in the two soil depths, the degree of competition between the tree and pasture for available N at different times of the year, or the amount of soil moisture present during the summer. The results of Hopmans and Flinn (1991) showed that radiata pine stem deformity was due to a high N availability, mainly as nitrate. However, the proportion of nitrate in the mineral N data from the Taheke ex-pasture site was unknown but the extraction of mineral N at Day 0 of the aerobic incubation (**Table 3.4**) indicated that the majority could have been nitrate.

The relationship between aerobic incubation data and stem deformity in February (**Table 3.7b**) was examined, since radiata pine stem deformities have been found to be most severe on improved legume pastures with high nitrification and minor on unimproved pastures showing low nitrification (Hopmans and Flinn 1991). It was hypothesised that the response of the Taheke ex-pasture soil samples to ammonium addition during the incubation would reflect the response of the soils in the field to the addition of urea-N. The results showed that increases in stem deformity positively correlated with increased nitrate production by the control samples and increased amounts of immobilised N in the amended samples. Higher levels of immobilised N (i.e. the reuse of nitrate produced in the short term) may reflect a larger and/or more active soil microbial population and thus, in the longer term, a greater ability to produce nitrate.

From the significance of the correlations it appeared that aerobic incubations may be of diagnostic use when identifying soils which are high risk for causing radiata pine stem deformities. But to separate the plots at the Taheke ex-pasture site into those most likely to produce tree deformities, based on the relationship between increasing stem deformity and number of kinks per tree with increasing nitrification or immobilisation would be difficult as indicated in **Figure 3.13**. It is possible that the amount of stem deformity observed at the Taheke ex-pasture site was negligible compared to those sites observed by Hopmans and Flinn (1991) where the potential nitrification of soils as estimated by aerobic incubations were also correlated with the degree of stem deformity.

There were a number of other nutrients, such as Mn (Carlyle *et al.* 1987, Shoemark 1988, Turner and Lambert 1991), aluminium (Turner and Lambert 1991) and sulphur (Birk *et al.* 1991) that have been associated with radiata pine growth deformities in Australian ex-pasture sites and agroforests, but were not measured during the Taheke ex-pasture field trial. Micronutrient antagonism has been found in both soil and plants. For instance, in the soil the behaviour of Cu, Zn, Mn and Fe appears to be the most antagonistic or synergistic in acidic conditions and in association with an increase in N supply, particularly nitrate (Turvey and Grant 1990). In the plant, Cu, with its variable valence (Cu^{+} and Cu^{2+}), behaves similarly to Fe and Mn which have similar ion diameter and atomic weight, and results in antagonism between the three micronutrients (Bussler 1981). As noted by Boardman

and McGuire (1990a) many nutrient interactions have been explained by the competition between chemically similar elements for a common metabolic pathway such as Zn^{2+} and Cu^{2+}. However, according to Turvey and Grant (1990) there is little evidence to link the behaviour of Cu and Zn in conifer nutritional physiology.

While foliar N and Zn concentrations, Cu:N ratios and soil N dynamics have shown significant correlations with radiata pine stem deformities at the Taheke ex-pasture site, it is likely that other micronutrients, such as Fe and Mn, may also be involved in the stem deformities - either affected by the high levels of soil N or Zn or antagonistic towards other micronutrients such as Cu both in the soil and the trees.

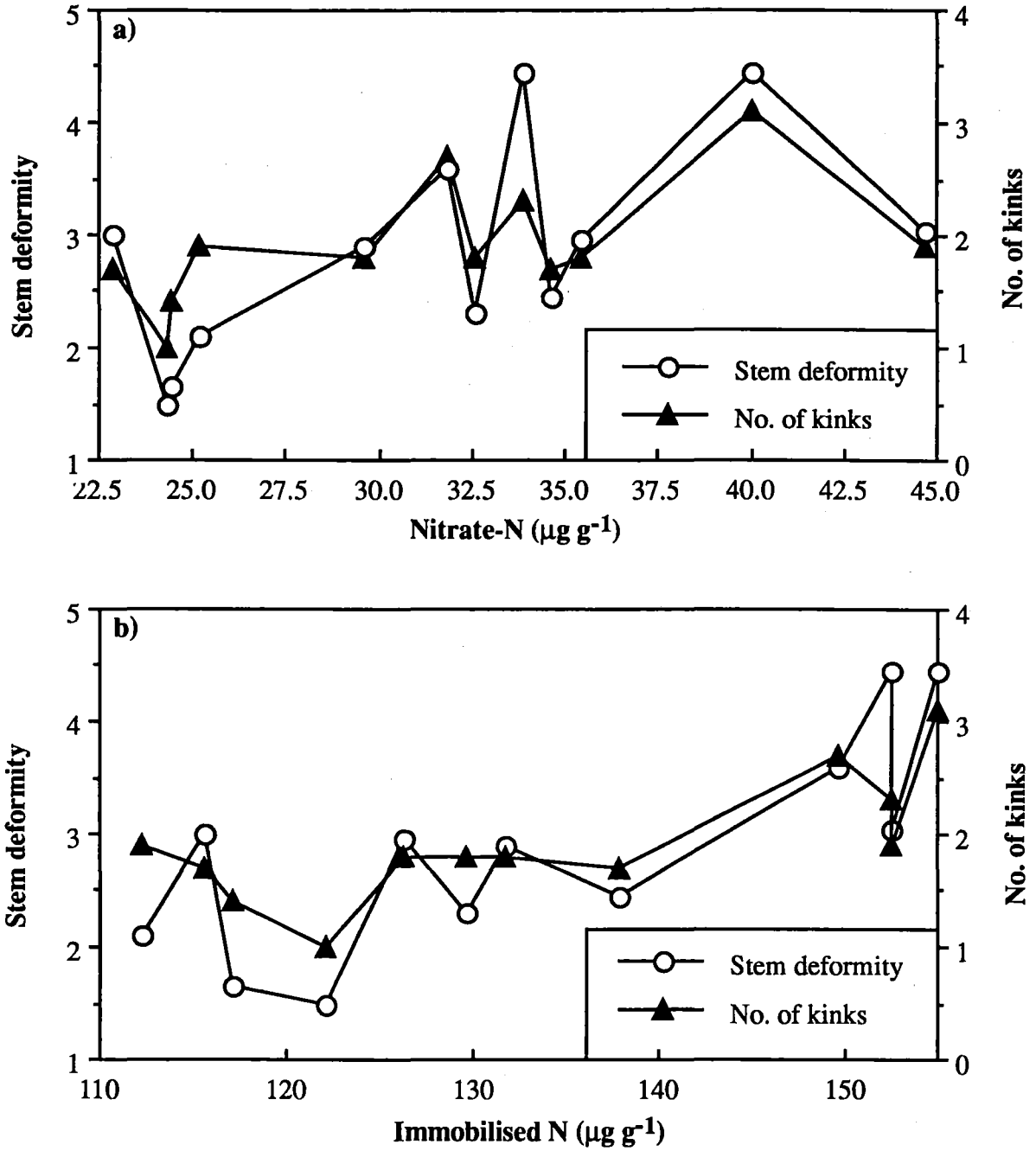


Figure 3.13: Correlations between plot means of stem deformity and the number of kinks at the Taheke ex-pasture site and a) increasing nitrate production by unamended soil samples and b) amount of N immobilised by amended soil samples in an aerobic incubation.

3.5 CONCLUSIONS

There were differences in the soil characteristics of the two sites sampled in Rotorua - the Taheke ex-pasture and pasture sites and the Whakarewarewa Forest site. The nitrification pathway at the Taheke ex-pasture site, and at the two pasture sites, was autotrophic with the predominant form of inorganic N being nitrate. For the conventional forestry site in Whakarewarewa Forest, the nitrification pathway may have been autotrophic and/or heterotrophic. As the pH of the soils at both sites were similar, soil pH did not appear to be the determinant of the type of nitrification pathway.

Soil profile studies indicated that the amount of nutrients such as total N%, Bray 2 extractable P and Bray 2 Mg were lower in the Whakarewarewa Forest soil profile. These differences were attributed to land-use history and variation in the types and depths of the volcanic parent materials which were a feature of these multisequal soils.

Added N only had a significant effect on foliar N% in the short term and significantly decreased the foliar concentrations of P, Ca and Mg during the trial. Increasing N addition had no significant effect on tree growth, the degree of stem deformity or soil N measurements. The major objective of this Taheke ex-pasture trial was to enhance a visually mild case of stem deformity in radiata pine by the addition of high rates of N. While the amount of stem deformity did increase during the trial period it was not a result of the N additions. At the Taheke ex-pasture site, the addition of N, even at the high rate of 500 kg ha^{-1}, was not a significant input into this system compared to the total amount of N already present in the topsoil.

Fates of the added N may have included microbial immobilisation, uptake by the pasture and incorporation on the soil exchange. Although the measurements of tree height, diameter and foliar N% were not significantly affected by N addition the tree canopies may have grown substantially in response to the added N. If this occurred, tree uptake may also have been a substantial fate of the added N.

The position of the plots within the trial site itself appeared to be the most important factor in determining tree growth and the level of stem deformity. There were indications that the soil nutrient status changed across the trial site as indicated by the differences in the two profiles sampled in the Taheke ex-pasture site. Although this may have been a function of natural soil variation the areas of increased tree growth, stem deformity and N and P foliar concentrations appeared to be associated with the area of the site represented by soil profile 1 which contained higher amounts of total N% and Bray 2 extractable P. This area was also at the base of a slope which may have improved the levels of soil moisture present.

There were significant correlations between the degree of stem deformity in February and the foliar concentrations of N and Zn, foliar Cu:N ratios and soil N measurements both from field samples and from laboratory incubations. High levels of total N% and mineral N in the soil correlated with trees of smaller height and DBH. The correlation with stem deformity and the number of kinks appeared to be dependent on the time of year - less stem deformity in August and greater stem deformity in February with increasing N, with the 0 to 10 or 0 to 20cm depths being the most significant.

It appears that a relationship between tree deformity and soil N characteristics may exist at the Taheke ex-pasture site. The ability of soils to nitrify and immobilise N in an aerobic incubation may indicate the susceptibility of the site to produce radiata pine stem deformities.

Chapter 4

The Ashley Forest field trial: The effect of N and B addition on fascicle nutrient contents and physical growth of young radiata pine growing on a low nutrient status soil.

4.1 INTRODUCTION

A number of workers have investigated the change in radiata pine needle nutrient concentrations with time. There appear to be two methods of needle sampling - the continual sampling of a particular age group of needle with time (Knight *et al.* 1983, Madgwick 1985) or following needle growth from its initiation (Fife and Nambiar 1984, Nambiar and Fife 1987). The first method produces information on changes in nutrient uptake by an age group of needles. The second follows the life of a needle - the pattern of needle growth and the movement of nutrients to and from the needle. The concentrations and contents of nutrients, such as N and P, in radiata pine needles change due to accumulation during needle growth, retranslocation during shoot growth, and replenishment from current uptake during periods of little shoot growth (Sheriff *et al.* 1986).

Nitrogen fertilisation and irrigation can substantially enhance growth in young radiata pine growing on poor soils with a low water-holding capacity (Raison *et al.* 1990). Unpublished data from Fife and Nambiar (1986, cited by Nambiar 1990) showed that the effect of N fertilisation was to decrease the frequency of fascicles per cm of branch, slightly increase the number of needles per fascicle and substantially increase fascicle weight. Neilsen *et al.* (1992) found that the repeated application of N to radiata pine growing on a shallow droughty soil resulted in large increases in wood volume, improved height growth, healthier trees, improved needle retention and needle mass, and increased foliar N levels. However macronutrient addition has also caused growth problems. Stone (1990) reported that macronutrient addition to and the drainage of peat soils may have been the cause of "growth disturbances" which were thought to be a result of an induced B deficiency.

In New Zealand, the effect of the addition of N and B fertilisers on radiata pine foliar nutrient concentrations has been investigated. Knight *et al.* (1983) set up a fertiliser trial (treatments were 168kg N ha^{-1}, 112kg P ha^{-1} and 22kg of B ha^{-1}) in winter in a 4 to 5 year old stand of radiata pine. Results from monthly foliage samplings showed that all of the nutrients in the foliage increased steeply a few weeks after fertiliser application, reached a peak in spring and declined during the summer. In the foliage, P concentrations stabilised and its effect was measured for at least 5 years compared to the control. The foliar concentrations of N and B declined. The N response lasted for about 11 months and the B response lasted for about 5 years.

Micronutrient availability is strongly influenced by soil properties such as organic matter content, pH and texture (J.A. Adams and R.G. McLaren, unpublished). While plants generally take up ionic forms of micronutrients from the soil solution, B is an exception being taken up as $B(OH)_3$, in acid soils, via the mass flow of water (J.A. Adams and R.G. McLaren, unpublished).

At Ashley Forest, the B status of the soils is considered to be marginal for radiata pine growth. This marginal B status may have been intensified by the windrowing of the site which will also remove the topsoil (Lambert and Turner 1977, Ballard 1978) as most of the B is found in the surface organic matter (Hill and Lambert 1981). J.A. Adams, Z. Hamzah, and R.S. Swift (unpublished) noted that

total and available B, in a number of Canterbury soils, increased with increasing organic matter status and clay content. Soils of the eastern South Island have a limited capacity to retain or buffer the effects of added B (J.A. Adams, Z. Hamzah, and R.S. Swift, unpublished).

In New Zealand there is a link between B deficiency and moisture stress (Will 1985) which is also influenced by topography and drainage status. The manifestation of deficiency symptoms is probably caused by reduced B uptake from dry soil surface horizons (Stone 1990). Rainfall and soil moisture are important in governing micronutrient availability to plants. In the soil solution, concentrations of micronutrients can change more than ten-fold, through rainfall, evaporation and plant transpiration, compared to much lower variations in the macronutrients such as Ca, Mg, K, Na, NO_3 and PO_4 (Kabata-Pendias and Pendias 1984).

Neilsen *et al.* (1992) found a strong correlation between radiata pine annual growth rate and annual rainfall for the last 5 years after the levelling off of a N fertiliser effect which produced large volume increases in the treated trees. Work in Australia has indicated that the critical level for B is rainfall dependent (Hill and Lambert 1981). Data presented by Turner and Lambert (1986) showed that the critical level for B decreases from about 11 to 5 $\mu g\ g^{-1}$ as the winter plus spring rainfall increased from 300 to 900mm. Rainfall also affects radiata response to fertiliser additions particularly if the summer is particularly wet or dry (Linder 1987). McGrath and McArthur (1990) found that during the summer, fertilised young radiata pine produced more dry matter than unfertilised trees.

As noted by Snowdon (1982) it is the soils capacity to maintain the availability of a nutrient to the plant, rather than the absolute amount of that nutrient in the soil, that is important. It appears that rainfall and moisture are important factors in controlling B availability to trees (Will 1985). Rainfall and the resulting soil moisture levels would be of importance at Ashley Forest where the annual rainfall of approximately 800mm (Fox *et al.* 1964) is quite low.

A variety of both short and long-term B fertilisers have been used to relieve B deficiency in radiata pine forests. Ulexite chips are considered to be the most suitable fertiliser for the long-term prevention of B deficiency in New Zealand (Will 1985). Will (1985) suggested that for plantation sites previously affected by B deficiency, 60 kg ha^{-1} of Ulexite chips (equivalent to 8 kg B ha^{-1}) should be applied 1 to 2 years after tree planting with further fertiliser applications should foliar B levels fall below 8 to 10 $\mu g\ g^{-1}$.

The aim of the trial described in this chapter was to investigate the effect of high rates of N addition and B addition on the growth and nutrient status of young radiata pine growing on a low fertility soil with marginal B status at Ashley Forest.

The response of radiata pine to the fertiliser additions was to be measured physically by tree heights, an assessment of stem deformity, and fascicle weights; and chemically by taking a number of fascicle samples, over the subsequent late spring and summer growing period, and measuring their nutrient concentrations and content.

4.2 MATERIALS AND METHODS

4.2.1 Field trial

In late spring of 1989, a field trial was set up in compartment 15 of Ashley Forest, North Canterbury (**Figure 4.1**). The trees were two year old radiata pine planted in an area where Douglas fir (*Pseudotsuga menziesii*) had previously been grown. Prior to planting, the site had been lightly root raked to remove the slash into windrows. The ground vegetation that subsequently developed consisted of gorse, broom, yorkshire fog, wildling radiata pine, and regenerating Douglas fir. Some areas of the site were still bare.

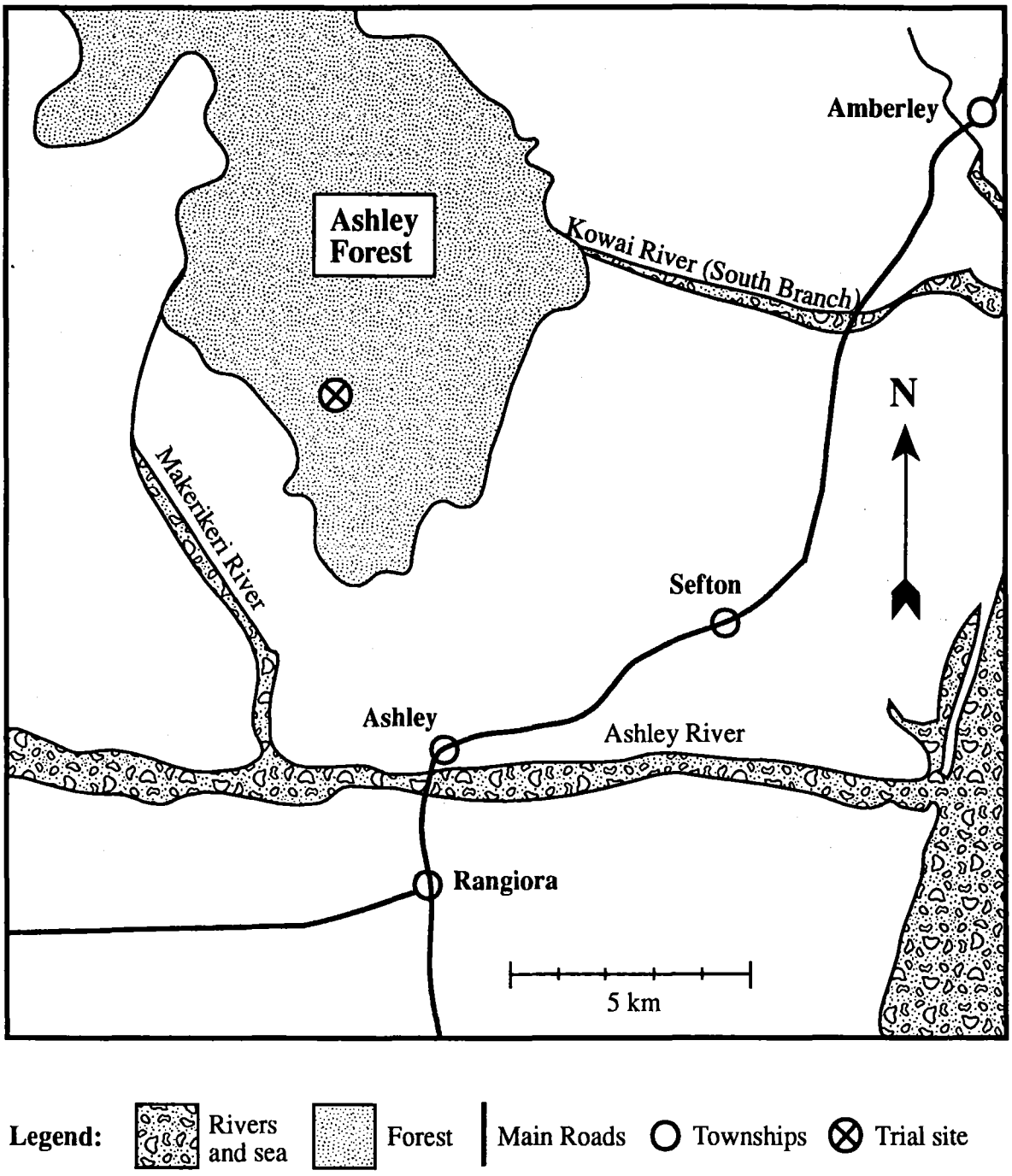


Figure 4.1: Map showing the location of Ashley Forest and the field trial site in Canterbury.

The soil was a Makerikeri hill soil. Fox *et al.* (1964) noted that the Makerikeri stony loam, found in Ashley Forest, was droughty on the ridges, of low fertility and was formed from greywacke conglomerate. A detailed analysis of soils at the Ashley Forest trial site is presented in Chapter 5.

The rows of radiata pine ran with the slope and had within-row spacings of 2m and between row spacings of 6m giving a stocking rate of 833 stems per hectare. The plots were 4m wide and 24m along the row (0.0096ha) to include at least ten trees in each plot. Four randomised blocks of the fertiliser treatments were set up across the trial site so that each block was on as uniform topography as possible.

The trial consisted of a factorial combination of 3 rates of N, at 0, 200, and 400 kg N ha^{-1}, applied as urea (46% N) and three rates of B, at 0, 3.7, and 7.4 kg of B ha^{-1}, applied as ulexite (14% B). A basal dressing of North Carolina rock phosphate, at 14 kg P ha^{-1}, was applied to all of the plots. This low rate of P was added to ensure that it was not a limiting nutrient at this site that affect the tree response to the fertiliser treatments.

4.2.2 Foliage sampling

Prior to the fertiliser application (1.11.89), a bulked foliage sample was taken from each plot. From each of the 10 trees in the plot, 10 fascicles were taken from just below the current growing point, from a north and a south facing branch in the upper-most whorl (i.e 200 fascicles per plot). These samples were oven-dried in paper bags at 70°C, weighed, ground (1mm) and stored prior to analysis.

Further foliage samples were taken during the summer and autumn, after the application of the fertilisers, in December (4.12.89), January (9.1.90), March (12.3.90) and May (12.5.90). These samples took the next 10 fascicles, above the area previously sampled on the branch, and were treated as previously described.

The plots in block 1 were also sampled approximately two years after the trial began (18.11.91). These samples took the next 10 fascicles, directly above the area sampled previously, on each of the two branches of each tree in the plots. Due to the biomass study (described in Chapter 5) some of the plots contained fewer than 10 trees. In these plots, all of the available trees were sampled.

4.2.3 Foliage analysis

For the analysis of the macronutrients N, P, K, Ca, and Mg, a wet digest with H_2SO_4/H_2O_2 was used. The basic method was that of Parkinson and Allen (1975) modified as described by Nicholson (1984). An Autoanalyser was used to measure the levels of N (indophenol blue) and P (vanadomolybdophosphoric yellow method) and K, Ca, and Mg were measured by atomic absorption spectrophotometry.

The levels of micronutrients Cu, Zn and B were found by dry ashing a 1.000g $\pm$ 0.002g of ground foliage sample in a silica crucible which was placed in a cold muffle furnace, heated to 600°C and the sample ashed for 1 hour. When cool, 10ml of 0.5M H_2SO_4 was used to extract the ash for 1 hour at room temperature. The solution was then filtered (Whatman 40) into a plastic vial. The Cu and Zn levels were measured by atomic absorption spectrophotometry. Boron was determined by the azomethine-H colorimetric method (Wolf 1971, Wolf 1974, Gaines and Mitchell 1979).

4.2.4 Physical tree measurements

Tree heights were measured in May 1990 using a height pole. A visual measure of stem deformity was also made, as described in **Table 4.1**, on the upper visible portion of the stem.

Table 4.1: The scoring system to determine the degree of stem deformity in young radiata pine trees at Ashley Forest.

Score	Comments	No.of trees
0	No kinking in the main stem, stem deformity = 0°	225
1	Very mild kinking, stem deformity = 0.125 to 0.25	100
2	Kinking, stem deformity = 0.25 to 0.5	29
3	Quite obvious deviations, stem deformity = 1+	5
4	Worst kinking, stem deformity = 5.5	1

The method of scoring:

$$Stem\ deformity = \sum(Deviation\ of\ kink_1 + \quad + Deviation\ of\ kink_x)$$

where the deviation is estimated as the amount, as a fraction of the diameter of the stem at the mid-point of the kink, that the kink deviates from the overall centre line of the tree.

4.2.5 Statistics

Data were subjected to analysis of variance (ANOVA) using the computer program GENSTAT. The following effects were examined:

(i) The effect of sampling date on the concentrations of nutrients in the control plots.
(ii) The effect of the increasing rates of N and B, and their interaction, on fascicle weights and nutrient concentrations and amount of nutrients in the fascicles at each sampling date from December 1989 to May 1990 and November 1991.
(iii) The effect of the increasing rates of N and B, and their interaction, on tree height and stem deformity in May 1990.
(iv) The effect of blocking on tree height and stem deformity in May 1990.
(iv) The effect of the increasing rates of N and B on the percentage of B retranslocated from the fascicles from January 1990 to March 1990.
(v) The effect of the increasing rates of N or B addition on fascicle weights and nutrient concentrations and amount of nutrients in the fascicles sampled from Block 1 in November 1991.
(vi) The effect of the increasing rates of N or B addition and sampling date on nutrient concentrations and amount of nutrients in the fascicles taken from Block 1 in May 1990 and November 1991.
(vii) The effect of the increasing rates of N or B addition on the change in nutrient concentrations and amount of nutrients in the fascicles taken from Block 1 from May 1990 to November 1991.

The Least Significant Difference (LSD) test was used to compare mean values.

The correlation coefficient (r) was calculated for each of the following paired observations using the computer program STATVIEW:

(i) Rainfall in the month prior to sampling and B concentrations in fascicles collected from the control plots from November 1989 to May 1990.
(ii) Rainfall in the month prior to sampling and B concentrations in fascicles collected from the a) N_0B_0 plots, b) $N_0B_{3.7}$ plots, and c) $N_0B_{7.4}$ plots from December 1989 to May 1990.

4.3 RESULTS

4.3.1 Climate

The climate data was from Rangiora (New Zealand Meteorological Service 1989, 1990).

The average annual rainfall at Rangiora is about 700mm while at Ashley Forest head quarters (4km from the trial site) the average annual rainfall is approximately 880mm according to Kear *et al.* (1967). The 1989/90 summer was especially dry with below normal monthly rainfall totals from December to May (**Figure 4.2**). During October, the rainfall was more than twice the norm, at 119mm, with near normal monthly rainfalls in December 1989 and March 1990.

The air temperatures through the summer and autumn were slightly warmer than normal (**Figure 4.3**).

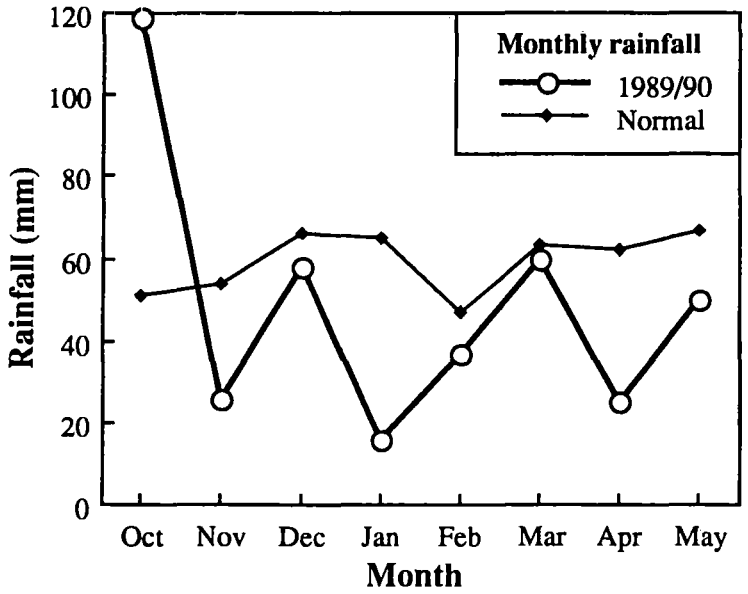


Figure 4.2: Normal October to May monthly rainfall and actual monthly rainfall during the 1989/90 summer at Rangiora.

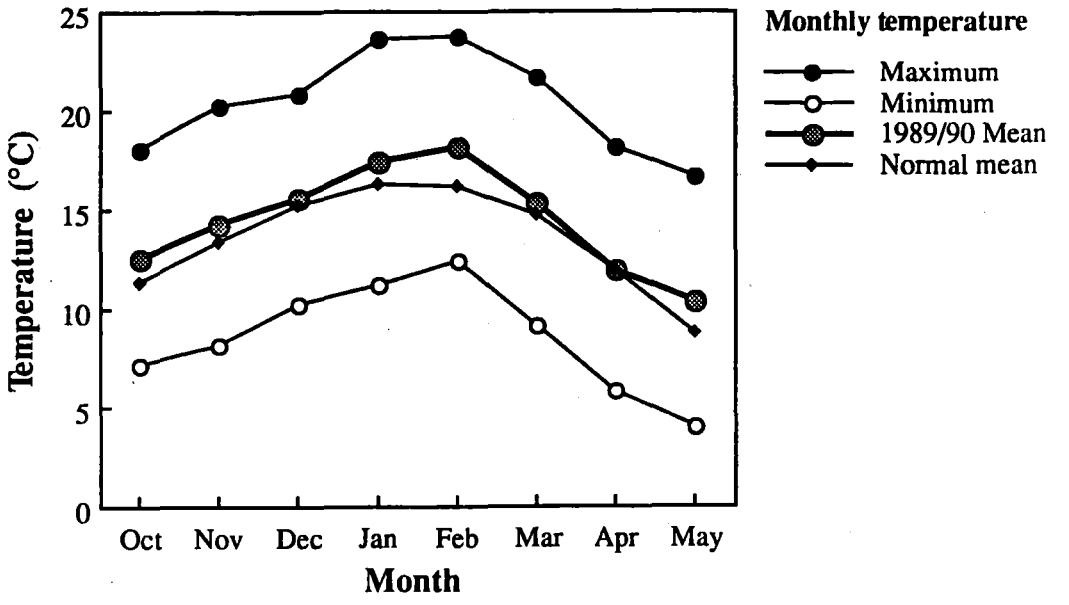


Figure 4.3: Air temperatures during the 1989/90 summer at Rangiora.

4.3.2 Foliage response

4.3.2.1 Changes in nutrient concentrations with sampling date in the control plots

In the control plots (N_0B_0) sampling date had significant effects on changes in the foliar concentrations of P ($p<.001$), K ($p<.051$), Ca ($p<.001$) and B ($p<.001$) in radiata pine (**Table 4.2**). The concentrations of both P and B significantly decreased from November to December, 1989, and again from January to March 1990. For B concentrations there was also a significant increase from December to January. After an initially high 0.39%, Ca concentrations significantly ($p<.05$) decreased to 0.21% and then significantly increased with each sampling date up to 0.49% in May. The concentrations of K fluctuated with sampling date however the concentration of 1.15% measured in December was significantly greater than the 0.83% found in May.

Table 4.2: Changes in nutrient concentrations of radiata pine foliage with time of sampling in the control (N_0B_0) plots at Ashley Forest from November 1989 to May 1990. For each nutrient concentration, means followed by the same letter were not significantly different ($p<.05$).

	November	December	January	March	May
N%	1.66 a	1.59 a	1.58 a	1.63 a	1.62 a
P%	0.235 a	0.189 b	0.176 b	0.120 c	0.118 c
K%	1.15 ab	1.09 a	1.01 ab	0.86 ab	0.83 b
Ca%	0.39 b	0.21 d	0.32 c	0.42 b	0.49 a
Mg%	0.127 a	0.131 a	0.114 a	0.126 a	0.128 a
Cu $\mu g\ g^{-1}$	5.5 a	4.5 a	4.6 a	5.0 a	4.5 a
Zn $\mu g\ g^{-1}$	28 a	26 a	27 a	30 a	32 a
B $\mu g\ g^{-1}$	92.1 a	10.7 c	32.3 b	11.3 c	12.8 c

The concentrations of N, Mg, Cu and Zn did not significantly change with sampling date in the control plots.

4.3.2.2 Comparison of nutrient concentrations with standard values

The nutrient concentrations found in March were similar to levels described as adequate for radiata pine (Will 1985). The concentrations of P in the N_0 rate were marginal at 0.120% (**Table 4.3a**). The increasing addition of N resulted in foliar P concentrations that were "low" (i.e less than 0.12%) and significantly ($p<.05$) less than the N_0 concentration. The lowest concentration of P in March was 0.079% for N_{400}. For all the N additions, the concurrent addition of $B_{7.4}$ appeared to promote the concentration of P (**Appendix 1a**).

In response to increasing N addition the foliar B concentrations in March were "satisfactory". The B concentration was only "marginal" (i.e. less than 12 $\mu g\ g^{-1}$) in the B_0 treatments (**Table 4.3b**).

4.3.2.3 The effect of the fertilisers from December to May

Fascicle dry weights in the control plots increased from an average of 12mg per individual fascicle in November to 89mg $fascicle^{-1}$ in May (**Figure 4.4**). As the control fascicle weights were not the maximum or minimum recorded from November 1989 to May 1990, the N and/or B fertiliser additions had had both positive and negative effects on fascicle weight.

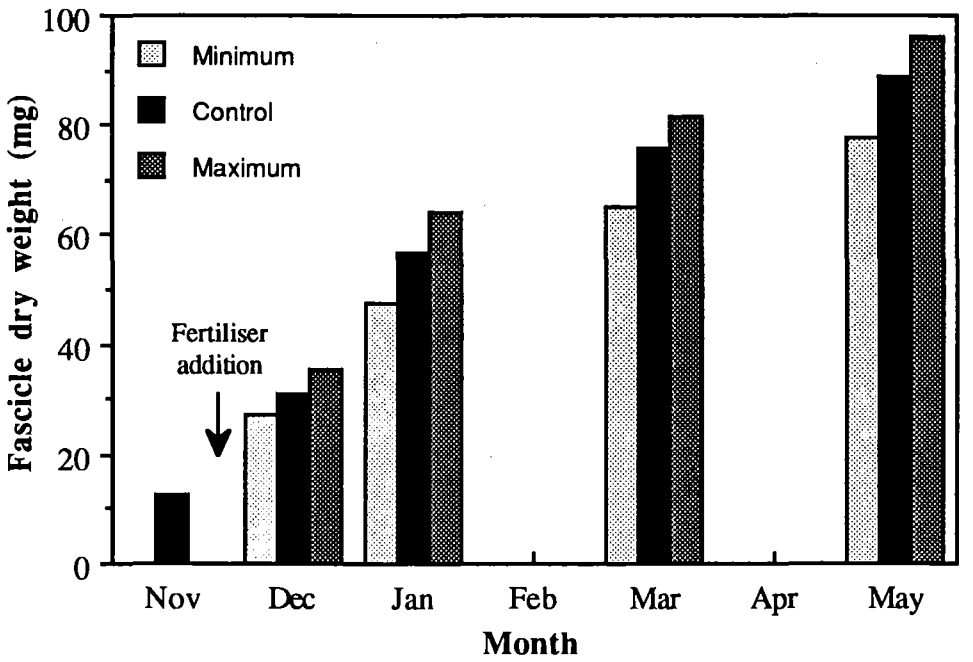


Figure 4.4: Effect of sampling date (November 1989 to May 1990) on the control (N_0B_0) fascicle weights and the overall minimum and maximum fascicle weights at Ashley Forest.

The addition of N had a significant and generally positive affect on radiata pine fascicle weights at Ashley Forest (**Table 4.4**). Compared to N_0, the addition of N_{200} significantly ($p<.05$) increased fascicle weights from January to May. The fascicle weights decreased as N addition increased from N_{200} to N_{400} but the decline was only significant in December. The N_{400} fascicle weights were greater, but not significantly so, than the weights at N_0 from January to May.

Table 4.3: Effect of increasing rates of a) N and b) B and the probability of a significant N or B main effect (NS = not significant) on the nutrient concentrations in radiata pine fascicles at each sampling date from December 1989 to May 1990 at Ashley Forest.

a)		N addition (kg ha^{-1})			Probability of N main effect	CV%
		N_0	N_{200}	N_{400}		
		--- % ---				
N	Dec	1.57 b*	1.71 a	1.73 a	<.001	4.1
	Jan	1.61 b	1.72 a	1.77 a	.002	5.9
	Mar	1.62 c	1.72 b	1.82 a	<.001	5.1
	May	1.61 b	1.70 b	1.84 a	<.001	7.0
P	Dec	0.192 a	0.184 a	0.179 a	NS	8.0
	Jan	0.170 a	0.154 b	0.141 c	.001	11.0
	Mar	0.120 a	0.090 b	0.079 c	<.001	12.0
	May	0.115 a	0.089 b	0.076 c	<.001	12.1
K	Dec	1.08 a	1.06 a	1.04 a	NS	5.5
	Jan	1.03 a	0.96 ab	0.88 b	.019	12.0
	Mar	0.92 a	0.74 b	0.76 b	<.001	12.0
	May	0.83 a	0.75 a	0.72 a	NS	20.3
Ca	Dec	0.21 a	0.22 a	0.22 a	NS	7.6
	Jan	0.31 a	0.30 a	0.31 a	NS	7.0
	Mar	0.42 a	0.41 a	0.40 a	NS	5.0
	May	0.47 a	0.46 ab	0.44 b	.002	4.4
Mg	Dec	0.129 a	0.134 a	0.130 a	NS	6.3
	Jan	0.115 a	0.108 ab	0.106 b	.072	9.0
	Mar	0.125 a	0.114 ab	0.109 b	.018	10.9
	May	0.121 a	0.111 ab	0.103 b	.013	12.3
		--- µg g^{-1} ---				
Cu	Dec	4.6 a	4.9 a	4.7 a	NS	8.6
	Jan	4.6 a	4.9 a	4.5 a	NS	8.9
	Mar	4.8 a	4.8 a	4.9 a	NS	7.8
	May	4.3 a	4.5 a	4.4 a	NS	8.6
Zn	Dec	26 a	27 a	26 a	NS	11.7
	Jan	27 a	28 a	26 a	NS	11.5
	Mar	29 a	28 a	28 a	NS	10.2
	May	31 a	29 ab	27 b	.063	11.5
B	Dec	13.2 a	13.1 a	12.4 a	NS	15.3
	Jan	33 a	32 a	33 a	NS	11.9
	Mar	17.8 a	16.3 a	13.3 b	.010	21.2
	May	21.0 a	19.4 ab	15.9 b	.016	22.0

4.3 b)		B addition (kg ha^{-1})			Probability of B main effect
		B_0	$B_{3.7}$	$B_{7.4}$	
		--- µg g^{-1} ---			
B	Dec	11.5 b	12.5 b	14.7 a	.002
	Jan	30 b	32 b	37 a	<.001
	Mar	9.9 c	14.9 b	22.4 a	<.001
	May	11.0 c	17.8 b	27.6 a	<.001

* For each nutrient, means followed by the same letter were not significantly different (p<.05).

Table 4.4: Effect of N fertiliser addition and the probability of a significant N main effect (NS = not significant) on the weight of radiata pine fascicles from December 1989 to May 1990 at Ashley Forest. For each sampling date, means followed by the same letter were not significantly different (p<.05).

	N addition (kg ha^{-1})			Probability of N main effect	CV%
	N_0	N_{200}	N_{400}		
	--- mg fascicle^{-1} ---				
Dec	31 ab	33 a	30 b	.051	9.7
Jan	53 b	62 a	56 ab	.058	14.3
Mar	71 b	79 a	77 ab	.050	10.5
May	84 b	94 a	91 ab	.082	11.7

From December 1989 to May 1990, added N had the most significant effect on nutrient concentrations and amounts of nutrient per fascicle (except for B) and there were two major trends in nutrient concentration response to added N alone.

The first trend involved the concentrations of N in the foliage which was the only nutrient to show a significant and positive response to increasing rates of N addition (**Figure 4.5**). Both the N_{200} and N_{400} rates increased N concentrations compared to the N_0 rate. After the initial increase in December with N_{200}, the N concentrations at this rate remained approximately 0.1% higher than the concentrations at N_0 while N concentrations in the N_{400} rate increased throughout the trial.

In the second significant trend, the increasing application of N appeared to have a negative effect on a number of nutrient concentrations particularly P and Mg. The foliar concentrations of P significantly (p<.05) decreased from January to May as the rate of N addition increased from 0 to 200 and 200 to 400 kg ha^{-1} (**Table 4.3a**). The concentrations of Mg at N_{400} were significantly (p<.05) less than those at N_0 with the concentrations at N_{200} not significantly different from N_0 or N_{400} from January to May.

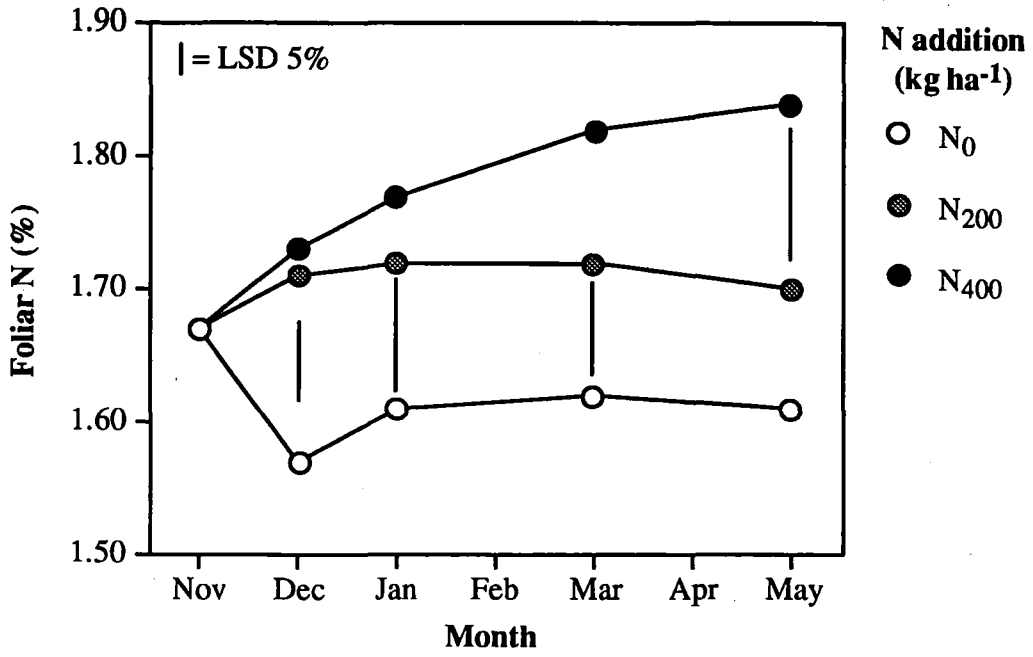


Figure 4.5: Effect of N addition on the concentrations of N in radiata pine fascicles at Ashley Forest from November 1989 to May 1990.

The concentrations of K, Ca, Zn and B were also affected by increasing N addition. The concentrations of Ca, Zn and B were significantly lower at N_{400} than N_0 in May (and also for B in March) while the N_{400} K concentrations in January and March and the N_{200} K concentrations in March were significantly less than the values at N_0.

From December to May, all nutrients, as amounts per fascicle, had a different response pattern to the addition of N (**Table 4.5**). Generally, in December there was a positive response to the addition of N_{200}. At this rate the amounts of N, P, K, Ca, Mg and Cu were significantly higher than the amounts in the N_0 and/or N_{400} rates. After December, only the amounts of P were significantly lower in the N_{400} rate than at N_0 or N_{200} in January and May while in March the amount of P in the N_{200} and N_{400} rates were significantly less than at N_0.

In May the amount of Mg and B was significantly lower at N_{400} while the amount of Cu fascicle^{-1} was the lowest in the N_0 rate in January and May.

By March, the addition of N_{200} and N_{400} significantly increased the amount of N in the fascicles compared to the N_0 rate.

From December to May, the addition of B alone significantly affected the concentrations and amounts per fascicle of B. With the increasing addition of B, the concentrations of B (**Table 4.3b**) and amounts of B fascicle^{-1} (**Table 4.5b**) significantly increased particularly in March and May.

Table 4.5: Effect of increasing rates of a) N and b) B and the probability of a significant N or B main effect (NS = not significant) on the amount of nutrient per radiata pine fascicle with sampling date from December 1989 to May 1990 at Ashley Forest.

a)		N addition (kg ha^{-1})			Probability of N main effect	CV%
		N_0	N_{200}	N_{400}		
		--- mg fascicle^{-1} ---				
N	Dec	0.48 b*	0.56 a	0.51 ab	.008	10.8
	Jan	0.86 b	1.06 a	0.99 ab	.011	15.9
	Mar	1.15 b	1.36 a	1.39 a	.001	11.7
	May	1.35 b	1.60 a	1.66 a	.002	12.8
P	Dec	0.059 ab	0.060 a	0.053 b	.047	11.8
	Jan	0.091 a	0.094 a	0.079 b	.043	16.4
	Mar	0.086 a	0.071 b	0.061 b	<.001	17.5
	May	0.098 a	0.084 a	0.069 b	.002	20.5
K	Dec	0.33 ab	0.35 a	0.31 b	.056	12.2
	Jan	0.55 a	0.59 a	0.50 a	.085	18.8
	Mar	0.66 a	0.58 a	0.58 a	NS	17.5
	May	0.71 a	0.72 a	0.66 a	NS	22.6
Ca	Dec	0.065 b	0.073 a	0.064 b	.016	10.5
	Jan	0.168 a	0.187 a	0.174 a	NS	17.3
	Mar	0.30 a	0.32 a	0.31 a	NS	11.6
	May	0.40 a	0.43 a	0.40 a	NS	12.4
Mg	Dec	0.040 b	0.044 a	0.039 b	.002	8.5
	Jan	0.061 a	0.066 a	0.059 a	NS	14.2
	Mar	0.087 a	0.089 a	0.083 a	NS	10.4
	May	0.100 ab	0.103 a	0.093 b	.053	10.6
		--- µg fascicle^{-1} ---				
Cu	Dec	0.140 b	0.159 a	0.140 b	.029	12.6
	Jan	0.24 b	0.30 a	0.26 ab	.021	18.5
	Mar	0.34 a	0.38 a	0.37 a	.066	12.1
	May	0.36 b	0.43 a	0.40 ab	.015	13.7
Zn	Dec	0.81 a	0.88 a	0.77 a	NS	15.3
	Jan	1.44 b	1.71 a	1.45 b	.018	15.8
	Mar	2.0 a	2.2 a	2.0 a	NS	13.0
	May	2.5 a	2.7 a	2.5 a	NS	13.0
B	Dec	0.41 a	0.43 a	0.37 a	NS	18.2
	Jan	1.75 a	1.98 a	1.85 a	NS	14.8
	Mar	1.27 a	1.27 a	1.04 a	.087	23.4
	May	1.79 ab	1.82 a	1.46 b	.082	24.4

4.5 b)		B addition (kg ha^{-1})			Probability of B main effect
		B_0	$B_{3.7}$	$B_{7.4}$	
		--- µg fascicle $^{-1}$ ---			
B	Dec	0.36 b	0.39 ab	0.45 a	.012
	Jan	1.68 b	1.82 b	2.08 a	.005
	Mar	0.78 c	1.11 b	1.70 a	<.001
	May	1.01 c	1.55 b	2.51 a	<.001

* For each nutrient at each sampling date, means followed by the same letter were not significantly different (p<.05).

4.3.2.4 Nitrogen and Boron fertiliser interactions

The only nutrient concentrations to exhibit a significant interactive effect of N by B were Mg in December (**Figure 4.6a**) and Ca in January (**Figure 4.6b**).

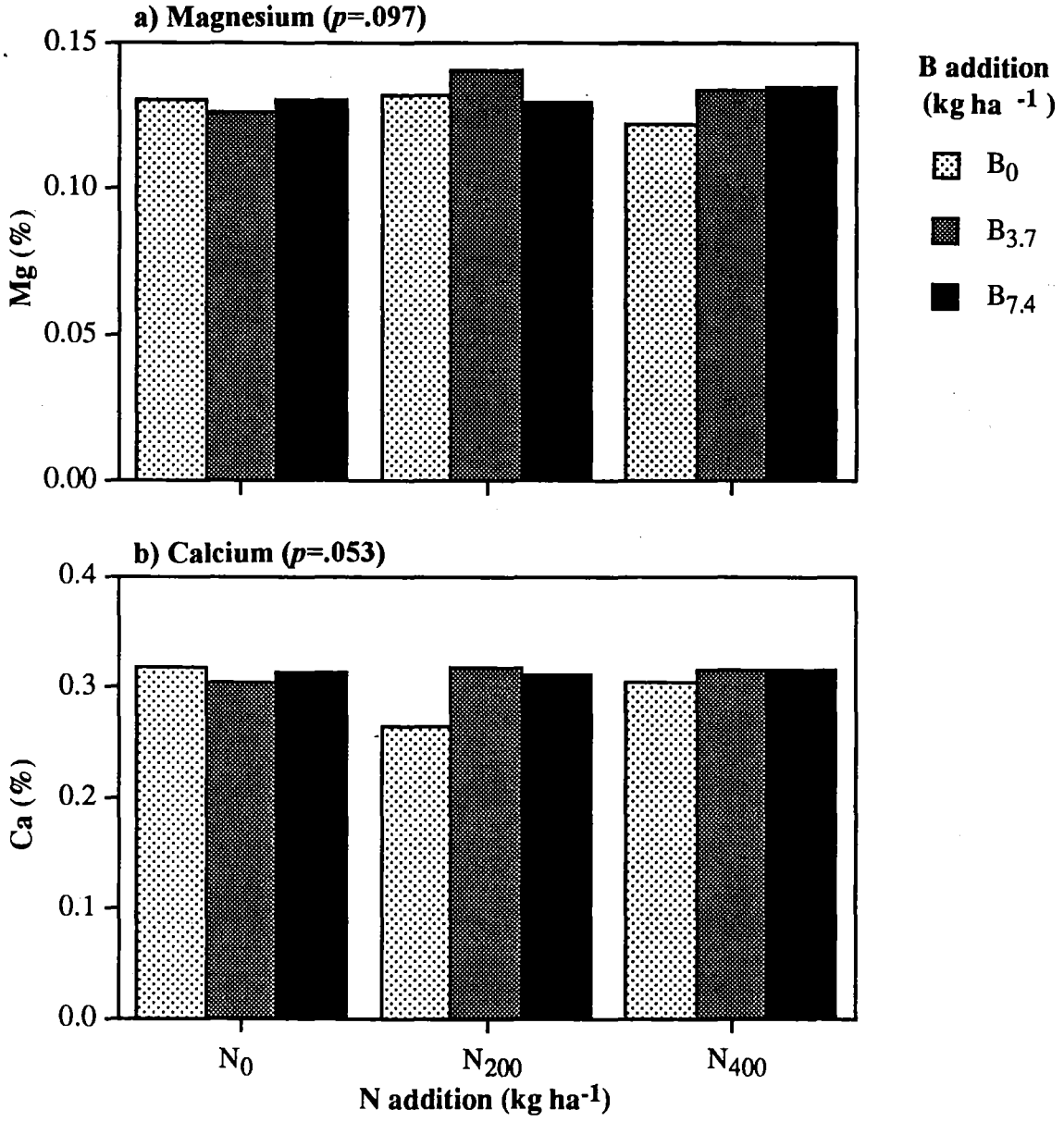
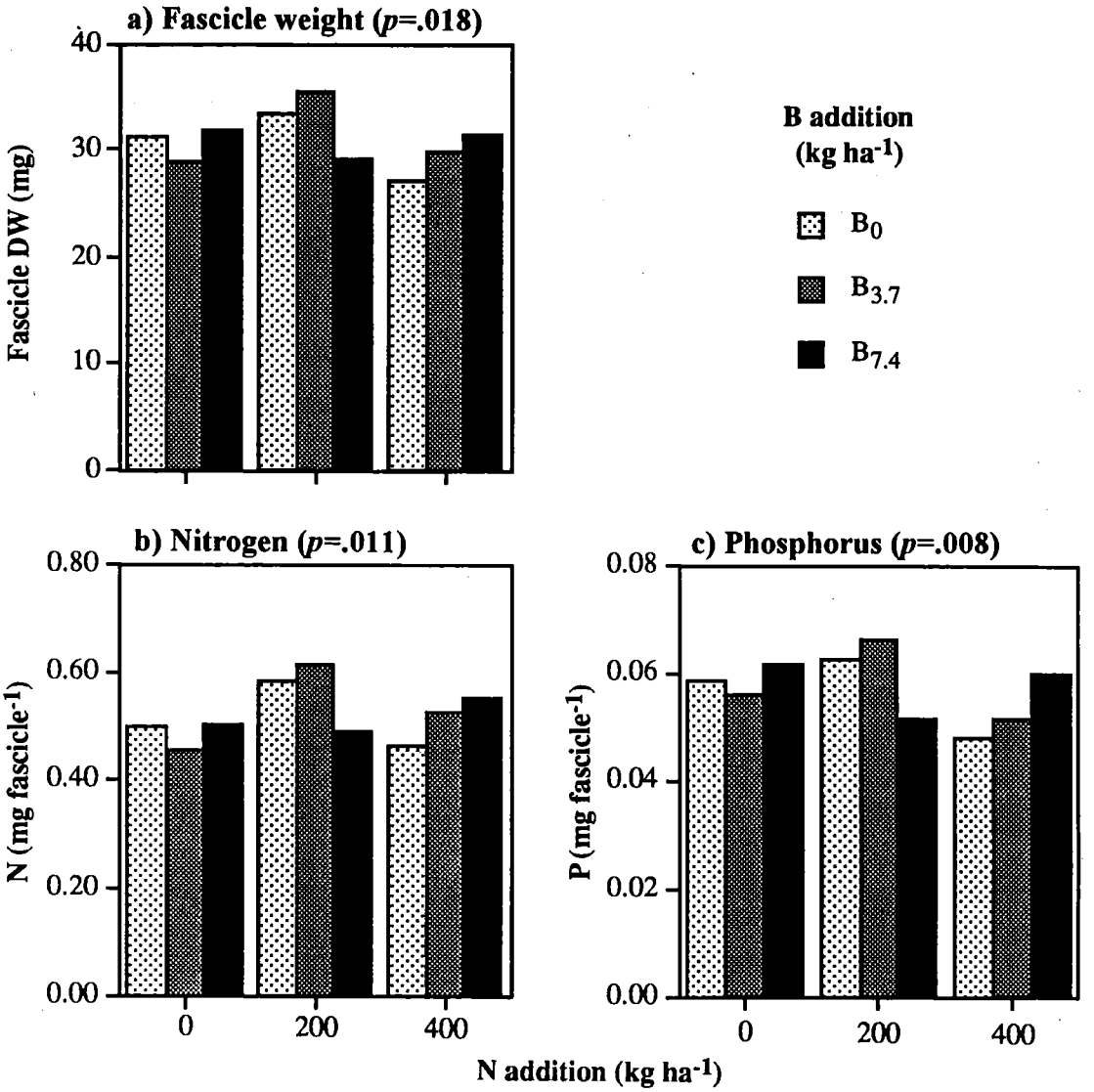


Figure 4.6: Significant interactions between N and B addition on the foliar concentrations of a) Mg in December and b) Ca in January at Ashley Forest. (See Appendix 1a for significant differences between the treatments).

The increasing addition of N did not significantly affect either nutrient (**Table 4.3a**). However in the N_{400} rate, the concentration of Mg significantly ($p<.05$) increased from 0.12 to 0.14% as the rate of B addition increased from 0 to 7.4 kg ha^{-1}. Within the N_0 and N_{200} rates there was no significant differences in Mg concentrations as a result of added B. In January the addition of B_0 in the N_{200} rate resulted in a Ca concentration that was significantly ($p<.05$) less than the Ca concentrations in all of the other treatments.

There were a number of significant interactions between added N and B which affected the amounts of nutrients in the fascicles in December and January, in particular, and also March.

In December, fascicle weights were significantly higher in the N_{200} than the N_{400} rate (**Table 4.4**). However, the addition of $B_{7.4}$ in the N_{200} rate significantly ($p<.05$) decreased the fascicle weight compared to the B_0 and $B_{3.7}$ rates (**Figure 4.7a**). In the N_{400} rate, increasing the addition of B from 0 to 7.4kg ha^{-1} increased fascicle weight (but not significantly) so that weight at $N_{400}B_{7.4}$ was not significantly different from the weight at $N_{200}B_{3.7}$.



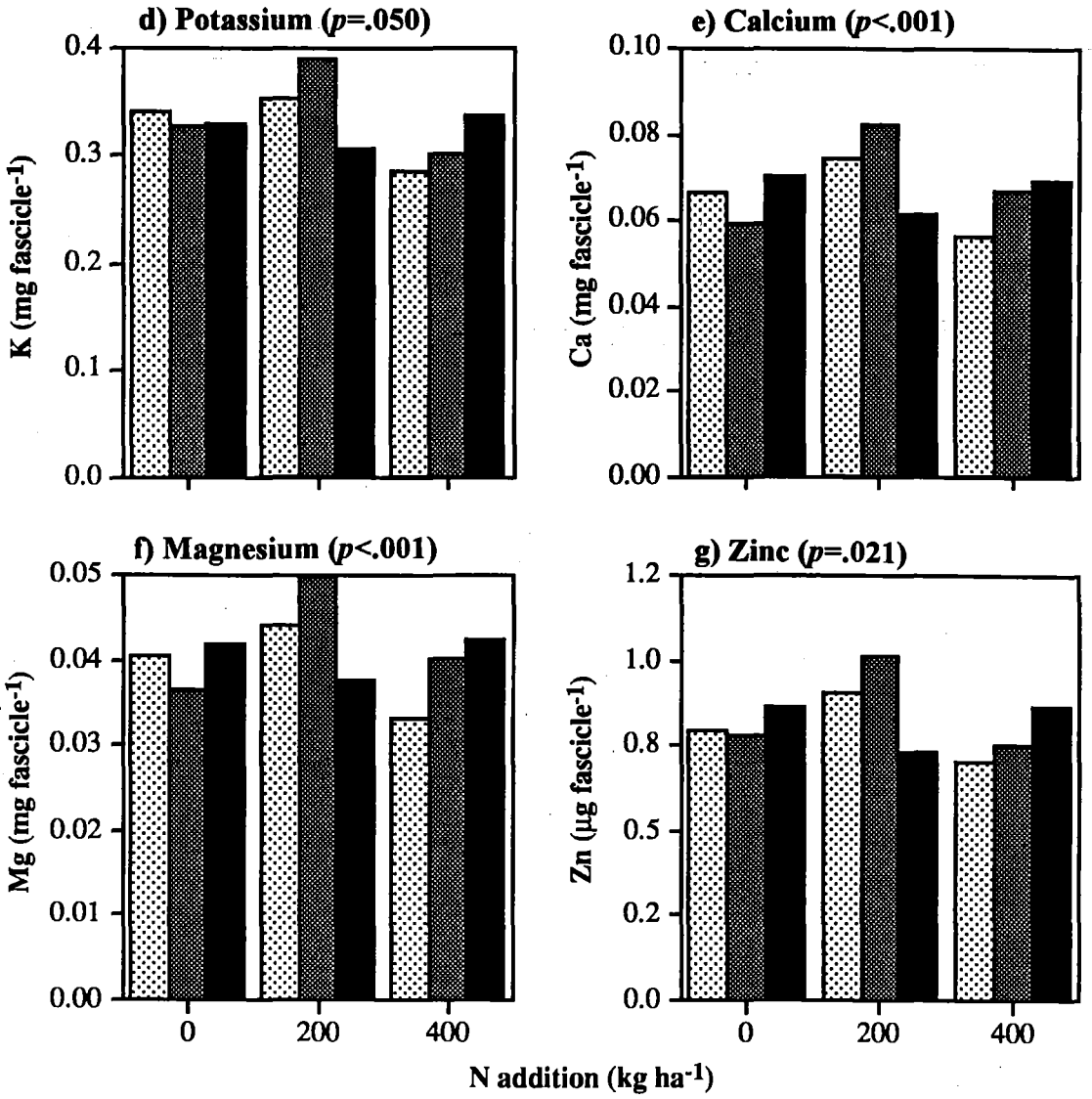


Figure 4.7: Significant interactions between N and B addition on fascicle weight and the amounts of nutrient per fascicle in December at Ashley Forest. (See Appendix 1b for significant differences between the treatments).

The trends exhibited by the amounts of nutrient per fascicle that were significantly affected by a N by B interaction (**Figures 4.7b to g**) were similar to the response of fascicle weights to N and B addition (**Figure 4.7a**). Only Ca (**Figure 4.7e**) and Mg (**Figure 4.7f**) had significant differences in their amounts per fascicle as a result of increasing B addition in the N_0 rate. In both cases the amounts were significantly lower at $B_{3.7}$ compared to $B_{7.4}$.

In January significant N by B fertiliser interactions affected fascicle weights and the amounts of P, Ca, Mg and B per fascicle. Within the N_0 rate the addition of $B_{3.7}$ resulted in a decrease in fascicle weight but the effect was not significant (**Figure 4.8a**). In the N_{400} rate fascicle weights were significantly higher with $B_{3.7}$ compared to B_0. The amounts of P (**Figure 4.8b**), Ca (**Figure 4.8c**), Mg (**Figure 4.8d**) per fascicle exhibited a similar response to that of the fascicle weights.

Within the N_0 rate the addition of $B_{3.7}$, compared to B_0, significantly ($p<.05$) reduced the amounts of P and Ca fascicle^{-1} while in the N_{200} rate the addition of $B_{3.7}$, compared to B_0, significantly increased the amount of Ca and Mg fascicle^{-1}.

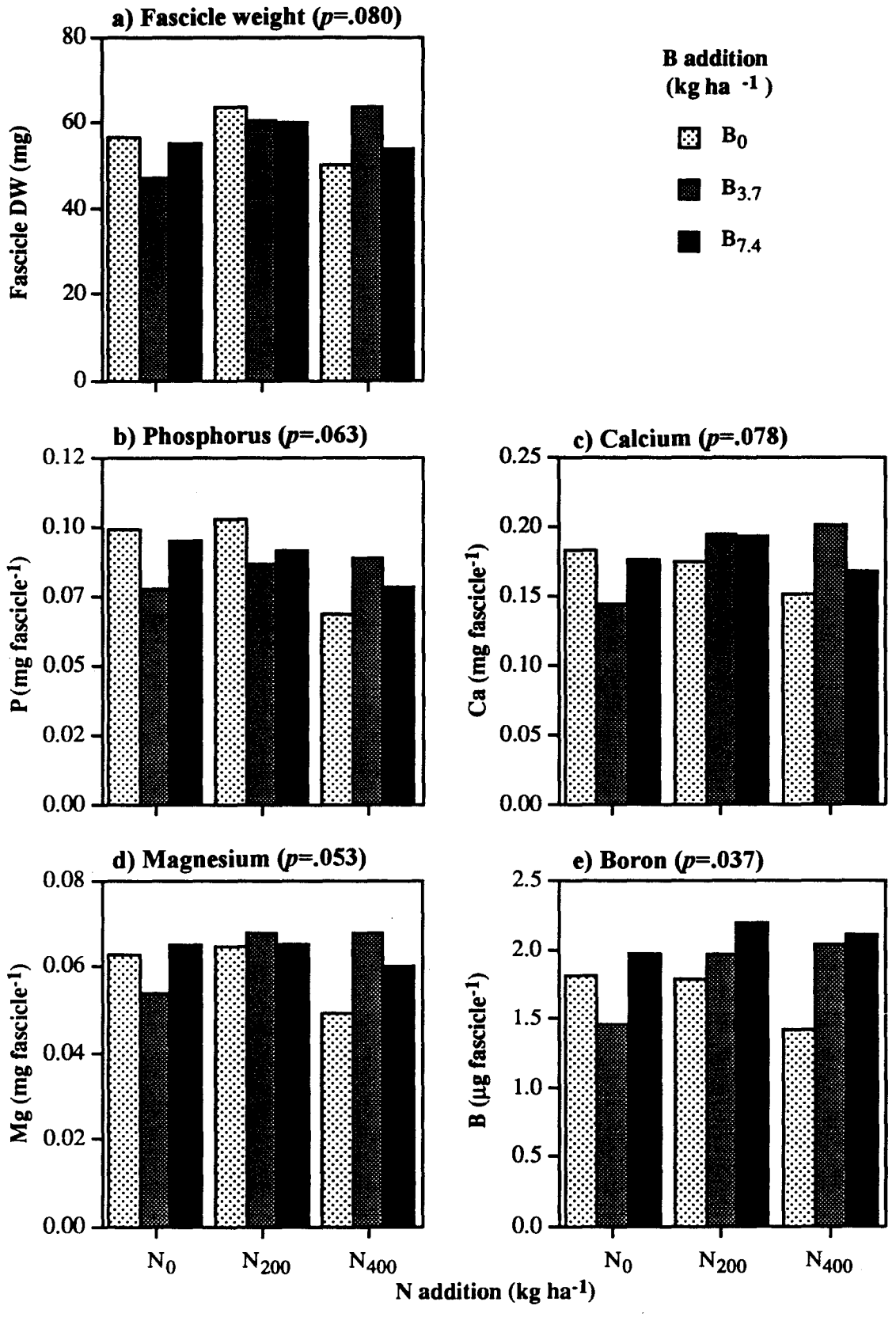


Figure 4.8: Significant interactions between N and B addition on the amount of nutrients per fascicle in January at Ashley Forest. (See Appendix 1c for significant differences between the treatments).

With increasing B addition the amount of B fascicle^{-1} increased (**Table 4.5b**). However, within the N_0 rate the amount of B in the fascicles decreased from B_0 to $B_{3.7}$ but the change was not significant. In N_{200} the increasing rate of addition from 0 to 7.4kg ha^{-1} did not significantly increase the amount of B fascicle^{-1}. In the N_{400} rate, an increase in B addition from 0 to 3.7kg ha^{-1} significantly increased the amount of B fascicle^{-1}.

In March, the interaction between added N and B significantly affected the amounts of Ca and Mg. While neither fertiliser had a main effect on these nutrients (**Table 4.5a**) increasing B addition from 0 to 3.7kg ha^{-1} in the N_0 rate significantly decreased the amount of Ca (**Figure 4.9a**) and Mg (**Figure 4.9b**) in the fascicles.

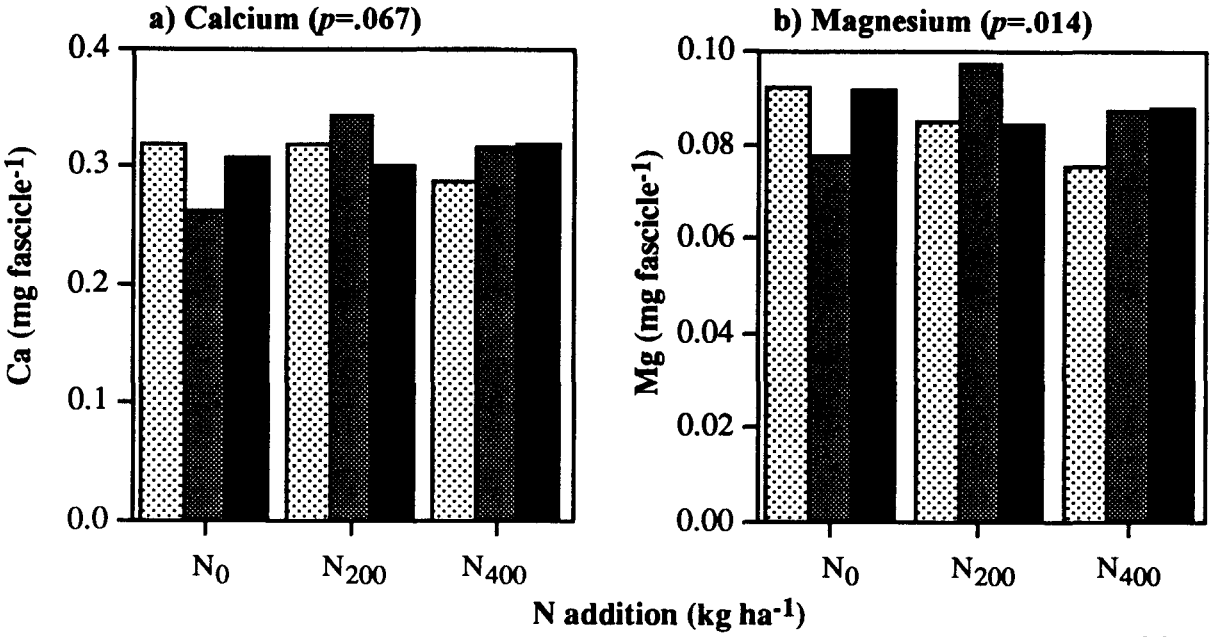


Figure 4.9: Significant interactions between N and B addition on the amount of nutrients per fascicle in March at Ashley Forest. (See Appendix 1c for significant differences between the treatments).

4.3.2.5 Two year needle sampling

After two years, significant fertiliser effects were present in the concentrations and amounts of nutrients in the fascicles sampled from Block 1 of the Ashley Forest field trial.

The concentrations of N, P and K were affected by N addition (**Table 4.6**). The N% was significantly higher ($p<.10$) for the N_{200} and N_{400} treatments compared to N_0, while the P% was significantly ($p<.10$) lower in the N_{200} and N_{400} compared to N_0. For K, the N_{400} treatment resulted in concentrations significantly less than the N_0 and N_{200} treatments.

The positive effect of B addition on foliar B concentrations was still evident with B concentrations for the $B_{3.7}$ and $B_{7.4}$ treatments being significantly ($p<.10$) higher than the 7.1μg g^{-1} at B_0. These two B treatments also significantly increased P% compared to B_0.

Table 4.6: Effect of N or B fertiliser on fascicle nutrient concentrations two years after addition to radiata pine at Ashley Forest. For each nutrient and fertiliser addition (N or B) means followed by the same letter are not significantly different ($p<.10$).

	B addition (kg ha^{-1})			**N addition** (kg ha^{-1})		
	B_0	$B_{3.7}$	$B_{7.4}$	N_0	N_{200}	N_{400}
			--- % ---			
N	1.17 a	1.13 a	1.15 a	1.08 b	1.13 a	1.23 a
P	0.045 b	0.067 a	0.064 a	0.074 a	0.049 b	0.052 b
K	0.51 a	0.48 a	0.46 a	0.53 a	0.51 a	0.41 b
Ca	0.45 a	0.47 a	0.45 a	0.48 a	0.48 a	0.41 a
Mg	0.103 a	0.099 a	0.110 a	0.111 a	0.106 a	0.095 a
			--- µg g^{-1} ---			
Cu	2.6 a	2.5 a	2.5 a	2.4 a	2.5 a	2.7 a
Zn	20 a	20 a	23 a	24 a	20 a	19 a
B	7.1 c	17 b	27 a	20 a	18 a	13 a
Fe	39 a	43 a	41 a	40 a	42 a	40 a

Fascicle dry weights showed no significant fertiliser effects (**Table 4.7**) and ranged from 59 to 99mg fascicle^{-1}, with a grand mean of 87mg. The addition of N had promoted fascicle weight from a mean of 77mg at N_0 to 95mg for the N_{400} treatment but the increase was not significant.

Table 4.7: Effect of N or B fertiliser on the dry weight (DW) and amount of nutrient per fascicle two years after addition to radiata pine at Ashley Forest. For each nutrient and fertiliser addition (N or B) means followed by the same letter are not significantly different ($p<.10$).

	B addition (kg ha^{-1})			**N addition** (kg ha^{-1})		
	B_0	$B_{3.7}$	$B_{7.4}$	N_0	N_{200}	N_{400}
			--- mg fascicle^{-1} ---			
DW	82 a	92 a	88 a	77 a	91 a	95 a
N	0.97 a	1.04 a	1.01 a	0.83 b	1.02 ab	1.17 a
P	0.036 b	0.060 a	0.057 ab	0.059 a	0.044 a	0.049 a
K	0.42 a	0.44 a	0.40 a	0.41 a	0.46 a	0.40 a
Ca	0.37 a	0.43 a	0.40 a	0.37 a	0.43 a	0.39 a
Mg	0.083 a	0.090 a	0.097 a	0.084 a	0.097 a	0.090 a
			--- µg fascicle^{-1} ---			
Cu	0.21 a	0.23 a	0.23 a	0.18 b	0.23 ab	0.25 a
Zn	1.65 a	1.86 a	2.01 a	1.84 a	1.83 a	1.84 a
B	0.58 c	1.53 b	2.35 a	1.63 a	1.65 a	1.17 a
Fe	3.1 a	3.9 a	3.6 a	3.1 a	3.8 a	3.8 a

The addition of N significantly affected the amounts of N and Cu in the fascicles. With N_{400} the amount of N, at 1.17mg, was significantly ($p<.010$) greater than the 0.83mg N fascicle^{-1} at N_0. The amount of Cu was also significantly promoted by N addition from 0.18µg at N_0 to 0.25µg Cu fascicle^{-1} at N_{400}.

The addition of B significantly affected the amounts of P and B. The amount of P for the $B_{3.7}$ rate, at 0.060mg, was significantly ($p<.10$) greater than the B_0 amount of 0.036mg P fascicle^{-1}. The amount of foliar B in the $B_{7.4}$ fascicles, at 2.35µg B fascicle^{-1}, was four times greater than the 0.58µg B fascicle^{-1} of the B_0 treatment **(Table 4.7)**.

Analysis of variance was used to assess the effect of the time of sampling and increases in N or B addition on the changes in nutrient concentrations and on the amount of nutrient per fascicle from May 1990 to November 1991 in Block 1 of the trial. Sampling time significantly affected the changes in the concentrations of N ($p<.001$), P ($p<.001$), K ($p=.049$), Cu ($p<.001$) and Zn ($p<.001$) which all decreased between May 1990 and November 1991 **(Table 4.8)**. Sampling time did not have a significant effect on the changes in B concentrations which declined only slightly from May 1990 to November 1991 for each B treatment.

Table 4.8: Nutrient concentrations and amounts in radiata pine foliage and fascicle weight (Wt) from two sampling dates in Block 1 of the Ashley Forest trial. Means followed by the same letter are not significantly different ($p<.05$).

	Wt	N	P	K	Ca	Mg	Cu	Zn	B
Concentrations:		--- % ---					--- µg g^{-1} ---		
May 1990		1.7 a	0.090 a	0.63 a	0.44 a	0.12 a	4.3 a	31 a	18.5 a
November 1991		1.2 b	0.059 b	0.48 b	0.46 a	0.10 a	2.5 b	21 b	16.9 a
Amounts:		--- mg fascicle^{-1} ---					--- µg fascicle^{-1} ---		
May 1990	75 b	1.3 a	.067 a	0.47 a	0.33 b	0.088 a	0.32 a	2.3 a	1.4 a
Nov. 1991	87 a	1.0 b	.051 b	0.42 a	0.40 a	0.090 a	0.22 b	1.8 b	1.5 a

Sampling time significantly affected the fascicle weight ($p=.040$) and the amount of N ($p=.015$), P ($p=.025$), Ca ($p=.027$), Cu ($p<.001$) and Zn ($p=.005$) per fascicle from May 1990 to November 1991. Fascicle weight and the amount of Ca per fascicle significantly ($p<.05$) increased **(Table 4.8)** while the amounts of N, P, Cu and Zn significantly decreased. The decrease was due to the decline in the concentrations of these nutrients.

There were no significant interactions between sampling time and N or B fertiliser addition on nutrient concentrations or amounts per fascicle.

Between May 1990 and November 1991 the only changes in nutrient concentrations or amounts per fascicle significantly affected by the fertiliser additions occurred for the amount of B fascicle^{-1} ($p=.099$) which was negative at B_0 and positive for $B_{3.7}$ and $B_{7.4}$ **(Figure 4.10)**.

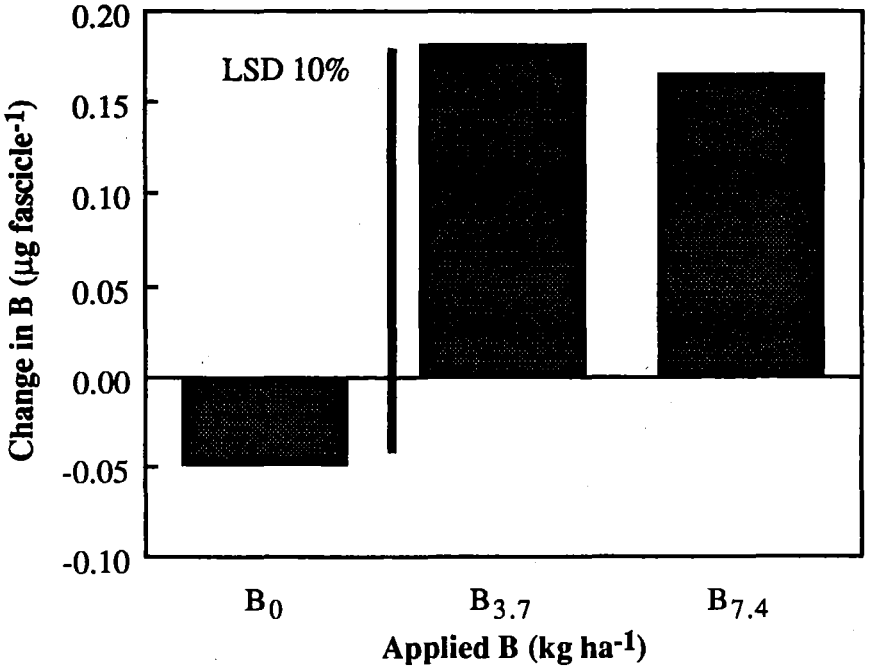


Figure 4.10: Effect of B addition on the change in the amount of B per fascicle from May 1990 to November 1991 at Ashley Forest.

4.3.3 Physical measurements at Ashley

4.3.3.1 Height

Tree heights were measured in May 1990 and showed no significant response to the addition of N and/or B fertilisers. The tree heights ranged from 1.3 to 3.8m with a mean height of 2.3m.

4.3.3.2 Stem deformity

In May 1990, the trees were scored for the amount of kinks that had appeared in the new growth of the main stem (**Table 4.1**). The Anova showed that the distribution of the data was skewed. While the range was 0.0 to 4.0, the overall mean was 0.50. Various transformations could not normalise the raw data so significant differences between the stem deformity means could not be calculated.

The means for each treatment indicated that the lowest level of stem deformity, 0.31, occurred in the control plots while the highest level occurred for the $N_0B_{7.4}$ treatment at 0.78 (**Table 4.9**). The amount of stem deformity per tree did not exhibit any trends that could associated with the increasing N or B fertiliser additions. At N_0, increasing B addition appeared to increase the amount of stem deformity while at N_{200} the stem deformity per tree decreased when B addition increased from 0 to 3.7kg ha^{-1}.

Table 4.9: Effect of N and/or B fertilisers on the level of stem deformity in young radiata pine trees at Ashley Forest.

	N_0			N_{200}			N_{400}		
	B_0	$B_{3.7}$	$B_{7.4}$	B_0	$B_{3.7}$	$B_{7.4}$	B_0	$B_{3.7}$	$B_{7.4}$
Stem deformity	0.31	0.58	0.78	0.65	0.38	0.38	0.43	0.53	0.48

4.4 DISCUSSION

4.4.1 Field trial site

The Ashley site was chosen for this trial because of its marginal B status for radiata pine growth and the low soil nutrient levels (see Chapter 5). It was considered that any radiata pine response to fertiliser additions would be measurable.

4.4.2 Tree growth response

The addition of N and/or B fertilisers had no significant effect on tree heights, by May 1990, or on fascicle weight during the sampling period. The blocking effect was the most significant ($p<.001$) factor explaining variation in the tree height data. The block means for height ranged from 204cm in Block 1 to 245cm in Block 4 with the tree heights in Blocks 2 and 4 being significantly taller than in Blocks 1 and 3 (**Figure 4.11a**).

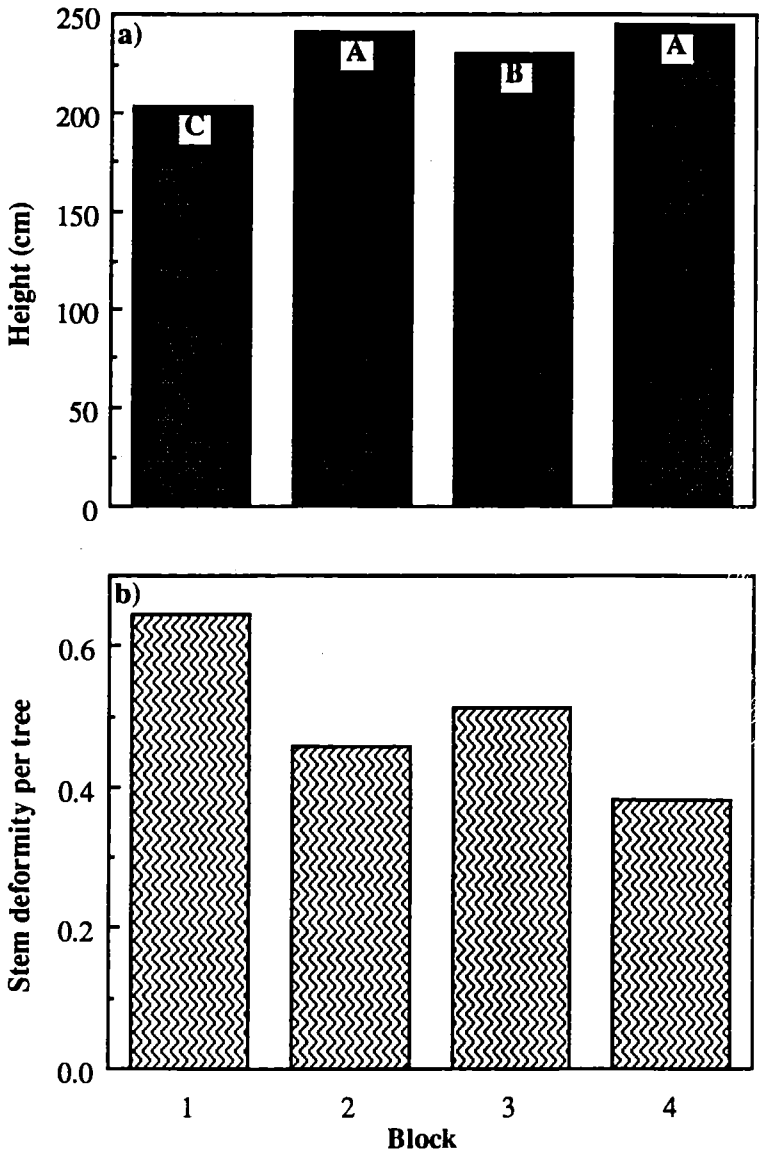


Figure 4.11: Blocking effect on the physical measurements of a) tree height and b) stem deformity of young radiata pine trees at Ashley Forest, May 1990. For heights, means with the same letter were not significantly different ($p<.05$).

Three years after the N and B fertiliser additions the heights and diameters of all the trees in the trial were measured (H. Aitken, pers. comm., 1992). The results showed that neither N nor B addition had significantly affected either tree measurement. The blocking effect was significant ($p<.001$) and the greatest tree heights (6.6 and 6.8m) and diameters (10.5 and 11.2cm) were measured in Blocks 2 and 4 respectively. Tree heights and diameters were significantly the lowest in Block 1 (5.5m and 8.7cm respectively).

Blocks 2 and 4 were further down the slope than Blocks 1 and 3 suggesting that soil and/or climatic factors were more favourable for tree growth down slope than near the top of the ridge. A characteristic erosional pattern occurs in the area resulting in soils that are shallow at or near ridge crests, deepening down slope until they become quite deep at the foot of the slope (Griffiths 1980). Fox *et al.* (1964) discussed the origins of Ashley Forest and reported that radiata pine grew well on the dry stony ridges as well as the deeper, wetter, more sheltered sites on the lower slopes. It appears that Blocks 1 and 2 of the Ashley Forest field trial may have been on shallow, droughty soils that would have lower amounts of nutrients, less capacity to hold soil moisture as well as being more prone to drying out during low rainfall periods compared to the soils associated with Blocks 2 and 4 which are likely to be deeper.

Sampling date was an important factor for the variation in fascicle weight during the trial. From November to May the fascicles greatly increased in weight with the rate of weight gain being highest in the first 2 to 3 months of growth. According to Nambiar (1990) most foliage growth in radiata pine occurs during spring/early summer where needles initiated in the spring attained a maximum weight of about 30mg needle^{-1} in 2-3 months. Madgwick (1985) found that in a 4-year-old stand of radiata pine in the central North Island new needles were measurable in September and attained maximum weight about 4 months later. The fascicle weights from this trial (**Figure 4.4**) suggest that radiata pine needle growth can continue for more than six months. This was confirmed by the results from Block 1 of the trial where fascicles sampled in November 1991 were significantly heavier than those sampled in May 1990 (**Table 4.8**). However, fascicle growth will be affected by such factors as rainfall and soil nutrient status. As both of these factors are low at Ashley Forest, needles may take longer to reach full extension.

The measurement of radiata pine stem deformity did not appear to be affected by N and/or B fertiliser additions. While the amount of stem deformity per tree ranged from 0.31 to 0.78 (**Table 4.9**), no obvious trends emerged from the data. There was, however, a difference in the Block means for the amount of stem deformity per tree (**Figure 4.11b**). Block 1 exhibited the highest level of stem deformity (0.64) while Block 4 had the least (0.38). Due to the skewed distribution of the raw data, the significance of these results could not be determined. It is interesting to note that Blocks 1 and 3 had both the smallest tree heights and the highest amount of stem deformity per tree. These results suggest that the amount of stem deformity per tree may also have been a function of variable site conditions as was suggested for the differences in tree height.

Plot averages of the amount of stem deformity per tree data were not skewed but an Anova did not identify any significant fertiliser effects or trends.

4.4.3 Foliage response

The method of progressively sampling fascicles up a branch - from just after initiation to full extension - was assumed to represent the 'life' of a fascicle during the late spring/summer/autumn

growing period at Ashley Forest. Each set of sampled fascicles was slightly younger than its predecessors. While this method of sampling was relatively simple, it is not known how accurately it describes the life of a fascicle or how such this method of sampling will affect the growth of the fascicles subsequently sampled.

There were a number of factors that affected the concentrations and amounts of nutrients present in the fascicles at Ashley Forest. The factors whose effect could be quantified were sampling date, the addition of N and/or B fertilisers and rainfall.

The time of sampling was the most important factor for explaining variation in the Anova for the nutrient data from November 1989 to May 1990. Sampling date was significant mainly because it charted large physical and chemical changes in the fascicles from just after initiation to near full extension. In order to keep pace with fascicle growth, the nutrient supply to the fascicle was maintained by tree uptake and internal retranslocation. Reductions in nutrient concentrations would have occurred through dilution within the extending fascicles and retranslocation from the fascicles.

Several trends were observed in the fluctuations of nutrient concentrations in the control plots as the foliage matured: 1) concentrations were initially high and then declined markedly e.g. for P and with fluctuations for B, 2) concentrations declined but not to a large degree e.g. steadily for K and with fluctuations for Cu, 3) the final concentration was higher than that in the newly formed needle e.g Ca and Zn where there was a drop in concentrations from November to December and then a steady increase until May, and 4) the nutrient concentration stayed at a relatively constant level with small fluctuations e.g. N and Mg (**Table 4.1**).

There are several explanations for the high concentrations of nutrients in the young November needles. For instance, the growing point may be a sink for nutrients and the young needles were initially 'charged' with nutrients whose concentrations were subsequently diluted as growth proceeded, supplemented by tree uptake and reduced by retranslocation. Also the nutrient concentrations may have been increased by the high October rainfall and later concentrations fluctuated with the amount of rainfall in the month prior to sampling. This explanation could account for the fluctuations in B and Cu concentrations where the rainfall in the month prior to sampling was significantly correlated with the B (p=.001) and Cu (p=.076) concentrations in the control foliage samples.

In reality, all the mechanisms controlling nutrient flux into and out of the fascicle, where the fascicle acts both as a nutrient sink and store, are affected by a number of factors including soil nutrient status, climatic factors such as rainfall, and the concentration, distribution and mobility of the nutrient throughout the tree. Distinguishing between dilution and retranslocation, as the cause of nutrient concentration decline in extending needles, is difficult. However, for dilution the amount of nutrient in the fascicle should remain the same while for retranslocation the amount of nutrient should decrease.

Nutrients can be retranslocated from needles before they are fully extended. Fife and Nambiar (1982) found that nutrients such as N, P and K can be withdrawn from radiata pine needles that are less than 5 months old. Nutrient data from this trial indicates that both dilution and retranslocation occurred for P and K where concentrations declined with sampling date, and therefore increasing fascicle weight, and also the amount per fascicle declined from January to March for nearly all the fertiliser treatments in the case of P and for all rates of added N and for K at the N_{200} rate (**Table 4.5a**). The amounts of B per fascicle also declined from January to March at all rates of added N

(**Table 4.5a**) and B (**Table 4.5b**) indicating that it was also retranslocated. Fife and Nambiar (1982) suggested that nutrients moved from spring formed needles to summer shoots as the drying of the soil and subsequent reduction in nutrient availability in summer may have increased the need for nutrient withdrawal. Therefore, the reasons for the withdrawal of nutrients measured by the March sampling may be related to the low rainfall levels in January and February 1990 (**Figure 4.2**). This appears to have been particularly significant for B. From March to May the amounts of P, K and B increased. Generally for P and B the amounts in May were less than the peak amounts in January.

The foliar nutrient data from November 1991 indicate that retranslocation of N, P, K, Cu and Zn had occurred in Block 1 since May as the amounts of these nutrients in the fascicles had decreased.

Apart from B, the uptake of other nutrients have also been shown to be linked to climatic factors. Turner and Lambert (1986) found that foliar P was affected by climate and that the rainfall in the 4 months before sampling gave the most significant relationship for prediction purposes. Fife and Nambiar (1982) described large fluctuations in the P content of pine needles in their first year which was caused by fluctuations in water availability. In this study rainfall may have been an important factor influencing initial P uptake in the control plots where the probability of a significant correlation between foliar P concentrations (from November to May) and the previous months rainfall was 0.119. However the significance of this correlation was dependent on the relationship between the high October rainfall and the high foliar P concentration in November (this was also the case for the significance of the correlation between Cu concentrations and rainfall in the previous month that was described earlier). With the addition of fertilisers the correlations between P (December to May) and the previous months rainfall were low and not significant. Thus at Ashley, rainfall in the month prior to sampling was not a good predictor of foliar P concentrations.

During the trial the N and B fertiliser treatments had a number of effects. Compared to where no fertilisers were added (i.e 0 rates), the foliar concentrations of N and B (**Tables 4.3a and 4.3b**) were significantly enhanced by the addition of the highest rate of the respective fertilisers for all sampling dates. The amounts of N and B in the fascicles (**Table 4.5a and 4.5b**) were also enhanced by the addition of the highest rate of the respective fertilisers particularly in March and May.

Treatment with B fertiliser had a significant effect on foliar B concentrations while N fertiliser application affected the concentration of N and other nutrients in the foliage. The significant effect of the N addition on non-fertiliser nutrients was negative for the concentrations of P, K and Mg and to a lesser extent Ca in May. It has been reported that N addition can decrease foliar P (Sheriff *et al.* 1986) while B addition can significantly enhance P uptake (Hopmans and Flinn 1984). In this trial, for each successive sampling date, the N fertiliser treatment became increasingly significant in its effect of reducing P concentrations with increasing rates of added N. The effect of N was increasingly significant on foliar Mg concentrations which were significantly lower in the N_{400} treatment compared to N_0, from January to May.

The addition of fertilisers appeared to affect the amount of P and B that was retranslocated during the period of January to March. At N_0, the amount of both P and B per fascicle declined by 5 and 27% respectively. With the addition of fertiliser the amount of P retranslocated increased. For instance, at the N_{200} rate (**Table 4.5a**) there was 0.094mg of P fascicle^{-1} in January and this decreased to 0.071mg in March. This represented a 24% decrease in the amount of P in the fascicle. These results suggest that fertiliser addition increased the proportion of P translocated between the January and March sample dates compared to the control treatment.

For B, the amount retranslocated from January to March was high, at 54%, where no B had been added (**Table 4.5b**). From 50 to 57% of the B that was present in the fascicles in January was retranslocated in the B_0 treatments (**Figure 4.12**). The percentage of B retranslocation from B_0 did not increase with increasing N addition but was reduced by the addition of B. Within the N_0 and N_{200} rates of N, increasing B addition dramatically reduced the percentage of B retranslocation. For N_{400}, there was no difference in the percent of B retranslocated at B_0 and $B_{3.7}$ although the actual amount of B retranslocated from these treatments was 0.76 and 1.05μg fascicle^{-1} respectively.

The large scale of reuse of P and B further highlights the importance of the two nutrients at Ashley. In March 1990 these were the only nutrients, of those measured, at less than satisfactory concentrations in the foliage. Radiata pine at Ashley Forest has shown a response to the addition of P fertilisers. Gordon and Graham (1986) reported that at age 11, the mean annual increment of radiata pine at Ashley Forest was increased from 1.84 to 2.74m^2 ha^{-1} yr^{-1} with the application of 100kg P ha^{-1}.

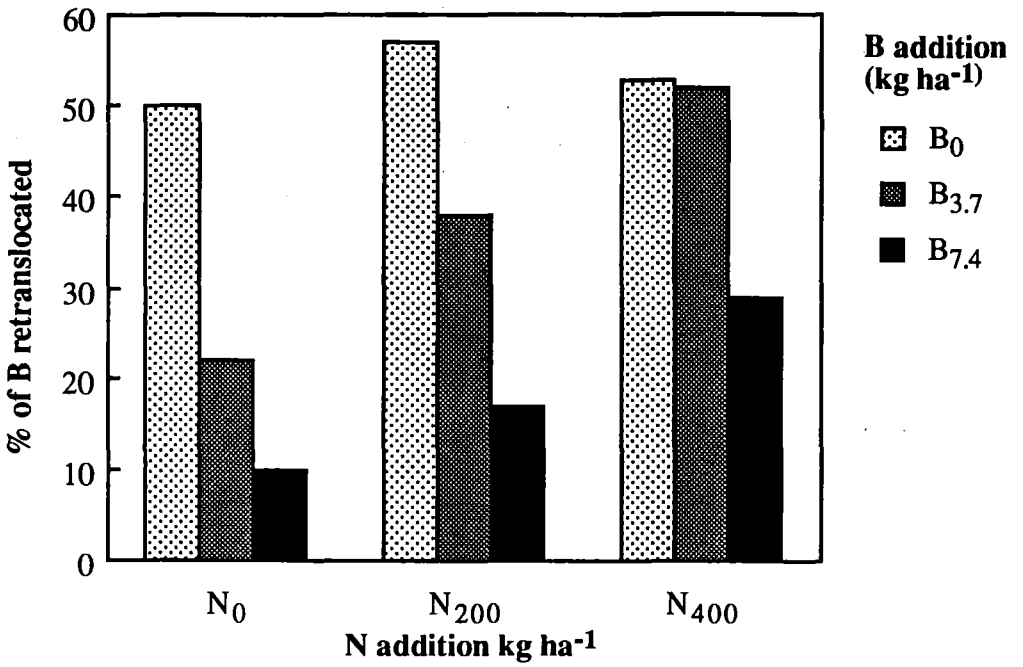


Figure 4.12: Effect of N and B fertiliser addition on the percent of B retranslocated from radiata pine fascicles from January 1990 to March 1990 at Ashley Forest.

The fertiliser treatments that increased nutrient concentrations and amount per fascicle depended in this study on the nutrient and changed with sampling date. The N_{400} rate significantly increased the concentrations and amounts of N in the fascicles. For foliar B, the addition of B at 7.4kg ha^{-1} had the most significant and positive effect on B concentrations and amounts. The amounts of P and K were the highest for N_{200} in December and January and the N_0 in March and May. For Ca, Mg, Cu and Zn the highest amounts at all sampling dates were found in the N_{200} rate. The positive response to N_{200} may have been a function of the greater biomass of the fascicles in this treatment.

4.4.4 Boron

At Ashley Forest the most important nutrient, from a tree nutrition and management point of view, is B. Ashley Forest has a history of marginal B deficiency in radiata pine which has been remedied by the addition of B fertilisers to young stands (H. Aitken, pers. comm., 1992).

In this trial, foliar B concentrations declined with increasing rates of N addition, increased with increasing B addition, and fluctuated substantially with time. In the Anova, sampling date was by far the most important factor followed by the addition of B fertilisers and then added N.

Without the addition of B fertilisers, B foliar concentrations at this site were marginal in March 1990 and the addition of N alone resulted in even lower B concentrations (**Table 4.3b**). The need for B fertiliser addition is apparent. Management practices at Ashley Forest include the aerial application of ulexite at 7.4kg B ha^{-1} when the trees are 2 years of age. In this study increasing rates of added B, in the N_0 plots, resulted in significant differences in foliar B concentrations (**Figure 4.13**). In December there was a significant ($p<.05$) difference between B concentrations in N_0B_0 and $N_0B_{7.4}$ treatments. In January the addition of B had no significant effect. This sampling date followed the near normal rainfall recorded in December after a drier than normal November (**Figure 4.2**). In March and May increasing B addition significantly increased foliar B concentrations with the B concentrations in the $N_0B_{7.4}$ plots being more than twice those in the control. The months prior to these sampling times, i.e. February and April, had lower than normal rainfall.

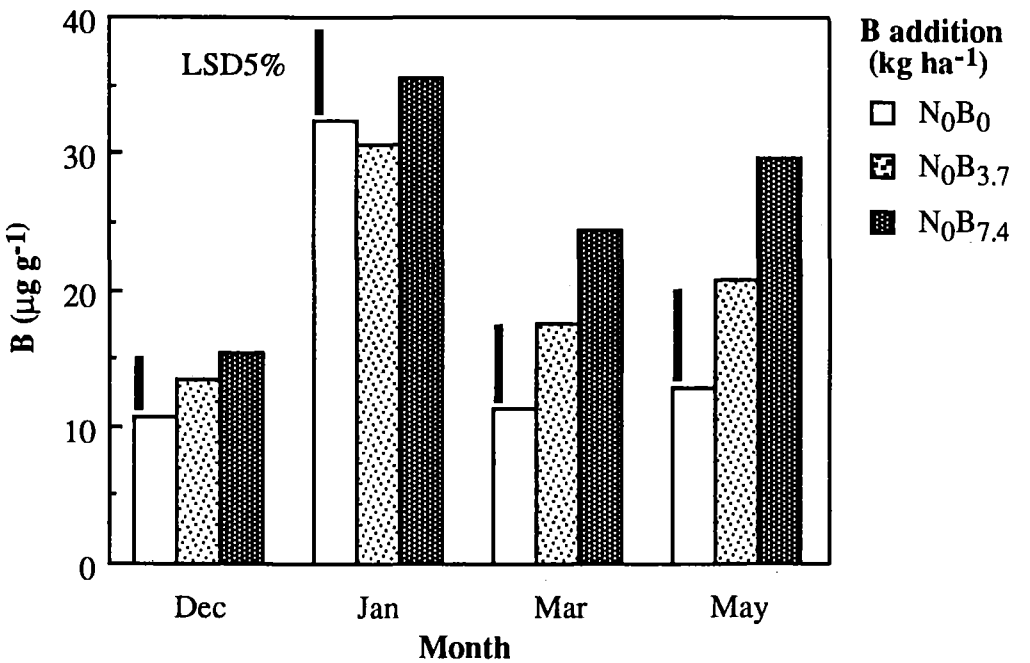


Figure 4.13: Effect of increasing B addition, at N_0, on B concentrations of radiata pine fascicles from December 1989 to May 1990 at Ashley Forest.

According to Hopmans and Clerehan (1991) annual fluctuations in foliar B were strongly correlated with rainfall during the preceding spring and summer. At Ashley the fluctuations of B - particularly the high B concentrations in November and January - appear to have been related to the amount of rainfall in the preceding month. The correlation between B concentrations in the control plot and the amount of rainfall in the month prior to foliage sampling was significant and positive (**Figure 4.14**).

This correlation was modified if B fertilisers had been added (**Figure 4.15**). It appears that the importance of rainfall on foliar B concentrations was reduced in those plots receiving B additions. For any given rainfall, foliar B concentrations were higher where $B_{3.7}$ or $B_{7.4}$ had been added and the correlation between B concentrations and rainfall in the previous month was not significant. However, in January after the near-normal rainfall in December, adding B fertiliser did not significantly elevate B concentrations above the control suggesting that soil moisture levels allowed for adequate B uptake even where B fertiliser had not been applied.

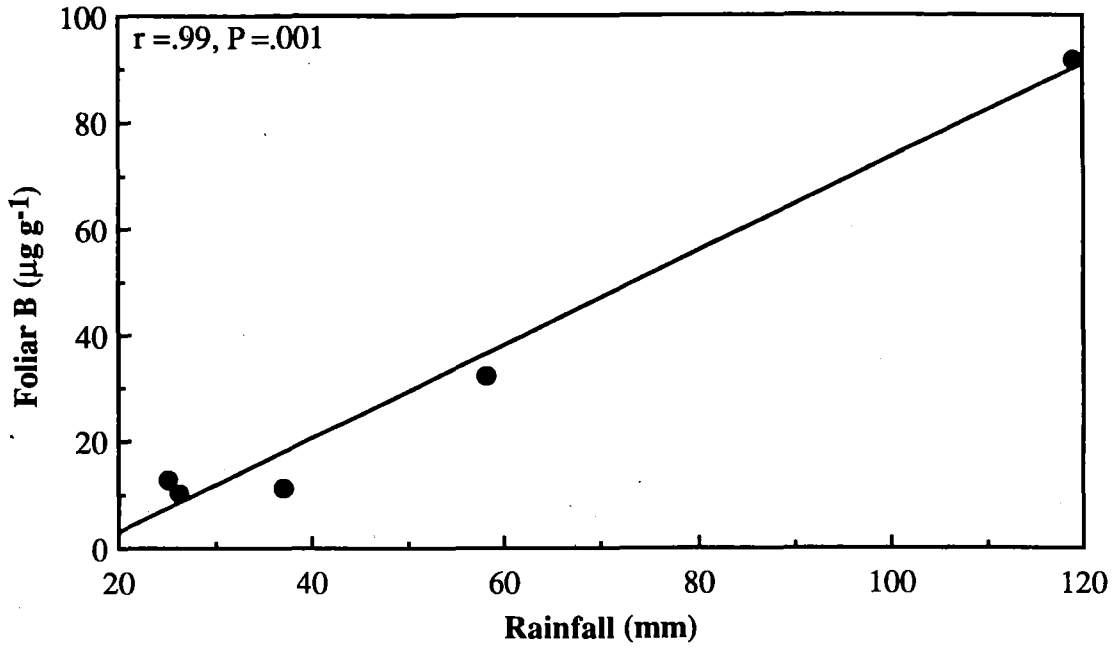


Figure 4.14: The correlation between radiata pine foliar B concentrations in the control plots (N_0B_0) and the previous months rainfall at Ashley Forest from November 1989 to May 1990.

It is interesting to note the decline in the concentrations and amount of B in the fascicles from January to March. B has been reported to be immobile once it reaches the foliage -it may move within the leaf but not be withdrawn from it (Stone 1990). However, unpublished data from M. Lambert (cited by Hill and Lambert 1981) indicated that B could be redistributed from older foliage to current foliage when the B supply was both adequate and limiting. Hopmans and Clerehan (1991) found that B redistribution will occur down to a limit of 5µg g^{-1} in radiata pine needles. The results in this study support these previous findings. As the amount of B declined the nutrient must have been withdrawn from the fascicles and retranslocated. The retranslocation of B even occurred in those fascicles that had received B fertiliser although the proportion that was retranslocated was less than where no B fertiliser had been applied. This mobility of B would be extremely important on a site such as Ashley Forest where the nutrient is present at low levels in the soil. Added B could be taken up at high levels by the tree and the nutrient would be available for further use within the tree especially when soil moisture conditions make it difficult for B to be taken up from the soil.

Of unquantified importance at Ashley Forest was the role of the large weed component in competing with the radiata pine for soil moisture and nutrients. It has been found that weed species which grow on B and S deficient sites usually have higher tissue concentrations of B and S than radiata pine on the same site so that weed suppression alone in such cases may alleviate nutrient availability problems (Lambert and Turner 1977) and result in an increase in foliar B (Mead and Gadgil 1978). The presence of weed competition may enhance the importance of rainfall in influencing the foliar concentrations of B at Ashley.

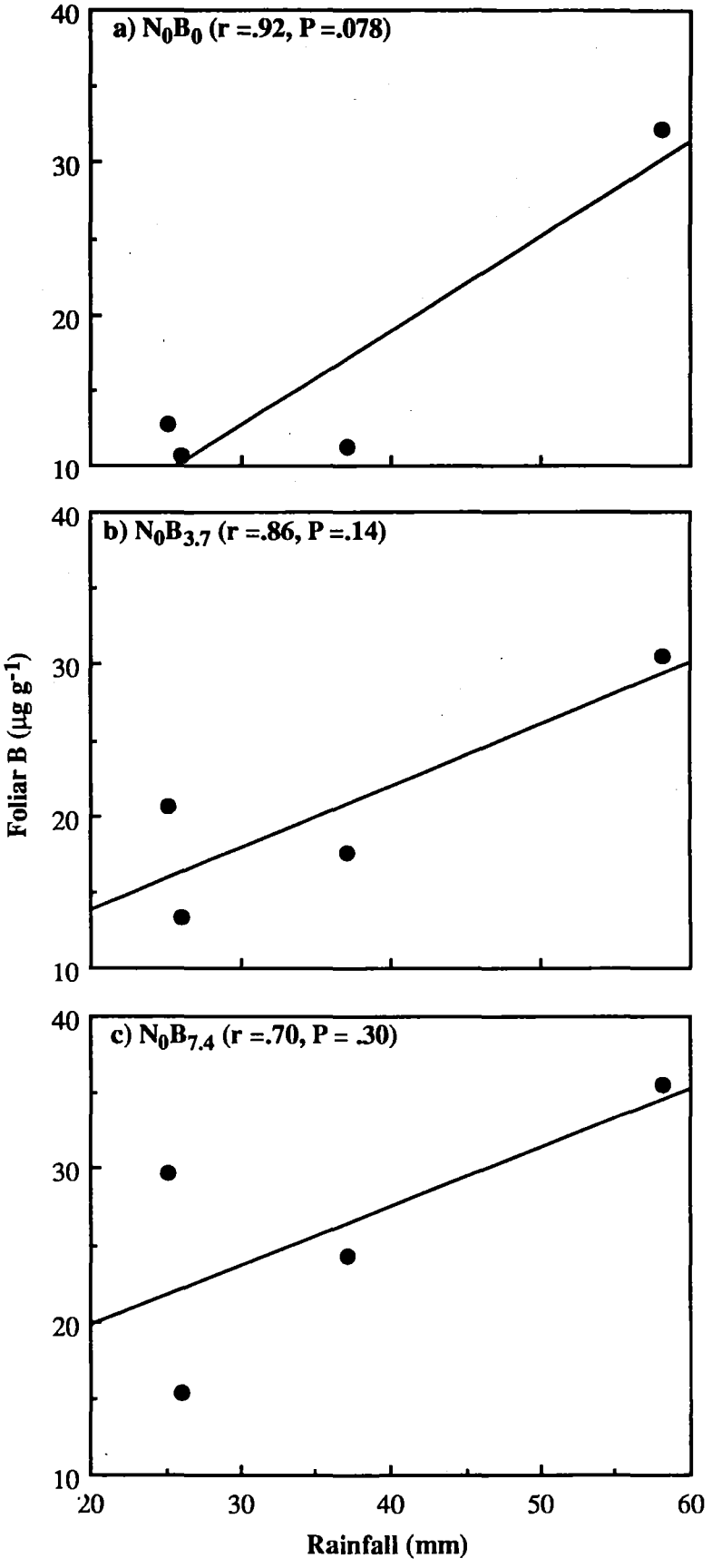


Figure 4.15: The correlation between radiata pine foliar B concentrations, affected by increasing B additions at N_0, and the previous months rainfall at Ashley Forest from November 1989 to May 1990.

4.5 CONCLUSIONS

Fertiliser additions did not significantly affect tree height growth but the addition of N at 200kg ha^{-1} significantly increased fascicle weights compared to the N_0 rate. The addition of N and B also had a significant effect on some of the concentrations and amounts of nutrients per fascicle. The addition of N significantly increased foliar N concentrations and the amounts per fascicle while B addition significantly increased B concentrations and amounts per fascicle. The significant effects on the non-fertiliser nutrients were mainly due to N addition and generally involved P and Mg whose concentrations and amounts per fascicle declined with increasing N addition. This negative affect of N was modified by the concurrent addition of fertiliser B. The addition of N generally had no significant affect on micronutrient concentrations and amounts per fascicle.

The additions of N and/or B fertiliser increased the amount of retranslocation of P and B from the fascicles. The results suggested that B was mobile and could be withdrawn from the fascicles when required, particularly during times of low soil moisture. The amount of B retranslocated was reduced where B fertilisers had been added.

It appeared that site factors, possibly related to the deepening of soils, an increase in soil moisture and a reduction in potential droughtiness, from the ridge top to downslope areas; may have affected radiata pine growth and the amount of stem deformity. The tallest and least deformed trees were measured on the downslope areas of the Ashley Forest trial site.

Environmental conditions, particularly the amount and timing of rainfall, appear to have been important factors in the uptake of nutrients, especially B, at this site. The influence of rainfall would be important from a diagnostic view point when assessing the requirement for B fertilisation on the basis of foliar B concentrations. The role of the weed competition at Ashley Forest may be an important factor affecting soil moisture and nutrient availability to the young radiata pine.

Chapter 5

The effect of nitrogen and boron fertilisers on the biomass of young radiata pine at Ashley Forest.

5.1 INTRODUCTION

There are two main areas that tree biomass studies have focused on: the production of biomass for energy and the distribution of nutrients within the trees themselves (e.g. Madgwick *et al.* 1977, Webber and Madgwick 1983, McColl and Powers 1984, Madgwick 1985, Pereira and Landsberg 1989). The production of biomass for energy and the subsequent removal of nutrients when the tree is harvested concerns only the above-ground parts of the tree while quantification of nutrient pools and fluxes involves investigation of the roots as well as other ecosystem components. This chapter is concerned with the investigation of fertiliser treatment effects on nutrient distribution within the above-ground parts of the tree.

In theory, a biomass study involves the harvesting and analysis of the whole tree. However, in practice many studies have only sampled the above-ground tree due to the difficulties of sampling the root system. The trees are generally divided into a variety of components such as needles, branches, stem wood and stem bark which may be further categorised according to age.

The New Zealand examples of radiata pine biomass studies have focused on a range of tree ages and measured a range of nutrient contents (**Table 5.1**) with micronutrients being analysed more recently in the biomass components.

Nutrient cycling and tree biomass studies provide background information on nutrient distribution, cycling between pools and nutrient demands with stand development (Ballard 1977) and reflects the changes in these nutrient pools as a result of fertiliser addition. Such changes in the tree nutrient status may reflect the luxury uptake and storage of the nutrients added as fertiliser and the dilution and retranslocation of those nutrients not added in the fertiliser.

Trees respond in a variety of ways to the addition of fertiliser. Examples are increased photosynthetic activity, expanded canopies and a change in the allocation of photosynthetic products (Binkley 1986). Nambiar and Fife (1987) found that N fertilisation increased the number and size of needles, rates of shoot production, stem volume and growth and the tree biomass of radiata pine growing on a soil containing low concentrations of mineral N. Nutrient fluxes into and out of the needles were also increased and the retranslocation of N, P, and K was increased as a result of the increased needle weight. Thus the tree response can be both physical through increased tree growth (e.g. Nambiar and Bowen 1986) and chemical via nutrient concentration changes.

According to Binkley (1986), after application, the general pattern of fertiliser distribution is to three areas: 1) into the tree which accounts for less than 25% of the added fertiliser in the first few years, 2) immobilisation in the soil microorganisms and soil organic matter which accounts for most of the fertiliser, and 3) losses via leaching and volatilisation which are variable and difficult to quantify. A proportion may also be found in competing vegetation such as weeds or, in an ex-pasture system, pasture plants.

Table 5.1: Some examples of *Pinus radiata* biomass investigations in New Zealand since 1960.

Authors and date	Tree age (Years)	Measured components	Nutrients analysed
Orman and Will 1960	26, 29	Needles, branches, bark and wood	N, P, K, Ca
Will 1964	10	Foliage, twigs, branches and stem	N, P, K, Ca, Mg
Madgwick *et al.* 1977	2 to 22	Stem wood and bark, live and dead branches, strobili, cones and 1-5 year-old needles	N, P, K, Ca, Mg, Na, Zn, Mn
Webber and Madgwick 1983	29	Stem wood and bark, live and dead branches, needle-bearing branches, cones and 1-4 year-old foliage	N, P, K, Ca, Mg, Zn, Fe, Mn, Al, S
Frederick *et al.* 1985	8	Stem wood and bark, live and dead branches, cones, twigs and needles	N, P, K, Ca, Mg, Mn, Zn, Cu
Cromer *et al.* 1985 a,b	10	Stem wood and bark, live and dead branches, cones, and needles (4 age classes, live and dead)	N, P, K
Madgwick *et al.* 1988 a	27	Stemwood	B, Cu, Mn, Zn
Madgwick *et al.* 1988 b	5 to 13	Stem wood and bark, live branches, 1 and 2 year-old needles	N, P, K, Ca, Mg, Cu, Zn, Mn, B

The difficulties associated with tree biomass studies include large sample volumes necessitating sub-sampling, the large number of samples per tree which must be analysed, categorising the tree components into age classes and sampling the root system.

For this study, trees were biomassed from the Ashley Forest field trial which had been set up 1 year previously to investigate the effect of rates of N and B on the growth and nutrition of young radiata pine. The biomass study was carried out to measure the change in tree growth due to fertiliser addition, to assess the fate of the added fertilisers within the tree and the soil and to measure changes in the nutrient concentrations of tree components.

5.2 MATERIALS AND METHODS

5.2.1 Tree biomass

Three trees were taken randomly from each of four treatment plots in a block of the Ashley Forest field trial laid down 1 year previously (Chapter 4). The sampled treatments were the control (N_0B_0), N added at 400kg N ha^{-1} with no added B ($N_{400}B_0$), B added at 7.4kg B ha^{-1} with no added N ($N_0B_{7.4}$) and both N and B added together ($N_{400}B_{7.4}$).

The trees were cut down at ground level and dissected into age classes (current to 4 year-old) of needles, branches, bark and stem (**Figure 5.1**). The bark was not removed from the current stem. Below ground, the stump and a portion of the roots were removed with the roots being washed and then divided into size classes based on their diameter - greater than 1cm, 0.25 to 1cm and less than 0.25cm. All of the samples were weighed (fresh), a weighed sub-sample was dried (60°C), reweighed, ground (<1mm for the bark and foliage, <2mm for the branch, stem wood, stump and roots) and analysed for their nutrient content.

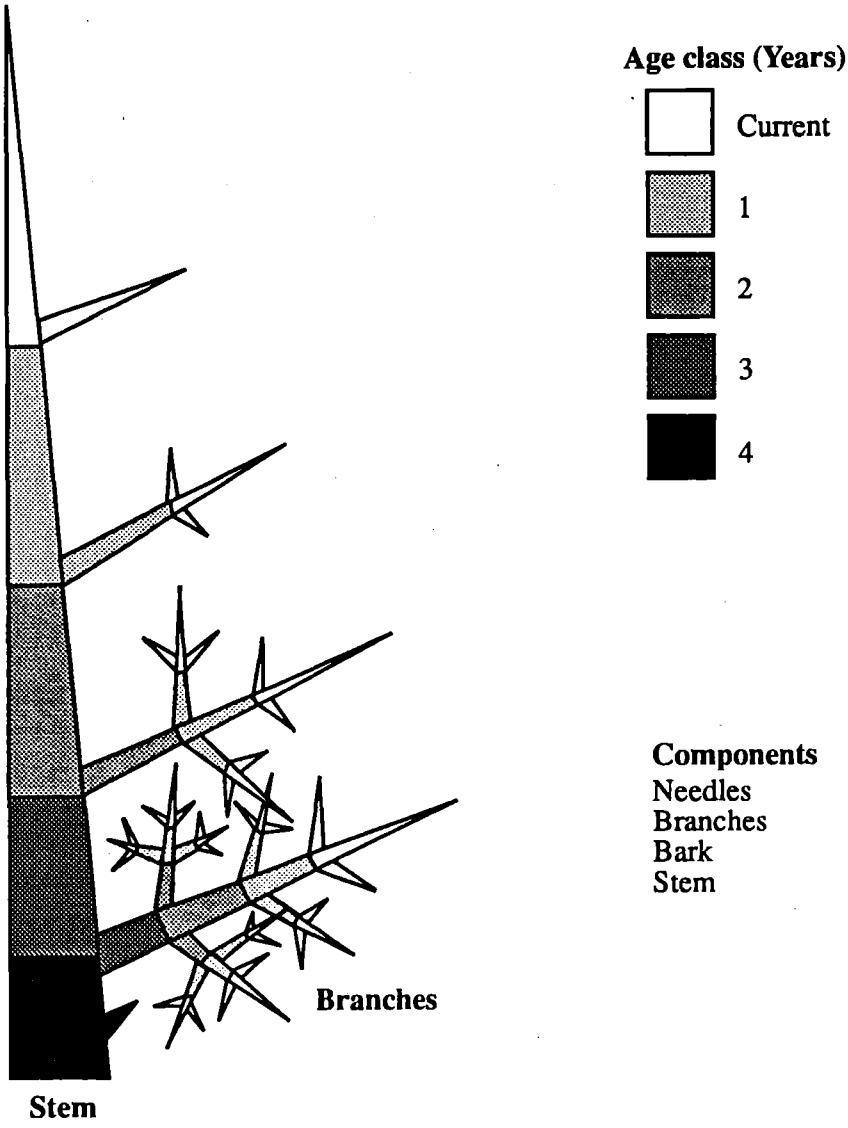


Figure 5.1: The partitioning of the above-ground tree into age classes during a biomass study of young radiata pine at Ashley Forest.

Macronutrient concentrations (N, P, K, Ca, and Mg) were found using a H_2SO_4/H_2O_2 digestion where N and P were measured on an auto-analyser and K, Ca, and Mg on a Shimadzu atomic absorption spectrophotometer as described by Nicholson (1984). The concentrations of micronutrients (Cu, Zn and B) were found using a dry-ashing technique at 600°C for 1 hour with the ash being extracted in 10ml of 0.5M H_2SO_4. The filtered (Whatman 40) solution was analysed for Cu and Zn contents by atomic absorption spectrophotometry and for B using the azomethine-H technique (Wolf 1974, Gaines and Mitchell 1979).

5.2.2 Soil Analysis

The soil was a Makerikeri Hill soil (yellow grey earth). Samples were taken from the sides of each pit, where the tree stumps had been removed, to a depth of 30cm in 10cm increments. The few stones that were present in the samples were discarded.

The samples were air-dried, sieved (<2mm) and analysed for pH, organic C%, total N%, Bray 2 P, and Bray 2 K, Ca and Mg according to the methods of Nicholson (1984).

Mineral N levels were found using an anaerobic incubation modified from Keeney and Bremner (1966) as described by Selvarajah *et al.* 1987. In duplicate, 10ml of distilled water was added to 5.0g of moist soil in a specimen jar which was sealed and incubated for 7 days at 40°C. The resulting levels of NH_4^+-N were found by adding 10ml 2M KCl, shaking end-over-end for 1 hour, filtering (Whatman 42) and analysing on the Autoanalyser.

The method for hot-0.02M $CaCl_2$-extractable B was modified from Parker and Gardner (1981) as described by Hamzah (1987). The resulting B levels were measured using the azomethine-H colorimetric method (Wolf 1974, Gaines and Mitchell 1979).

A B fractionation scheme (see Chapter 6 for methodology) was used to determine the distribution of B in the soil and the presence of residual B from the ulexite addition.

5.2.3 Statistics

Data were subjected to analysis of variance (ANOVA) using the computer program GENSTAT. The following effects were examined:

(i) The effect of the increasing rates of N and B on the weight of each tree component.
(ii) The effect of the increasing rates of N and B on the nutrient concentrations and amount of nutrients in each tree component.

The Least Significant Difference (LSD) test was used to compare mean values.

The correlation coefficient (r) was calculated for each of the following paired observations using the computer program STATVIEW:
(i) Soil and tree nutrient levels.

5.3 RESULTS AND DISCUSSION

There are a variety of processes that may affect the loss or conservation of added fertilisers to a site. At Ashley, losses of added N and B may have occurred via leaching through the soil profile, runoff down the slope and the volatilisation of N. Conservation of the added N and B could occur through plant uptake - both in the trees and weeds - and through the retention of the nutrients within the soil profile. This biomass study provided information on the presence of nutrients mainly in the above-ground tree and the upper soil profile and the effect that the fertilisers had on tree growth.

5.3.1 Rainfall

The monthly rainfall data from the Rangiora Meteorological Station (New Zealand Meteorological Service 1989, 1990) are presented in **Figure 5.2**. The trial period was drier than normal. From November to October the following year a total rainfall of 700mm is normal at Rangiora. However from November 1989 to October 1990 the actual rainfall was 515mm and only the August 1990 rainfall was greater than normal.

The amount of rainfall would influence the dissolution of the fertiliser, particularly the slowly-soluble ulexite, and the level of soil moisture which affects nutrient availability. For instance, McGrath and McArthur (1990) added N and P fertilisers to 1 year old radiata pine and found that during the summer the fertilised trees produced more dry matter than the unfertilised trees. Fertilisation can improve radiata pine growth efficiency if soil water is available (Linder 1987).

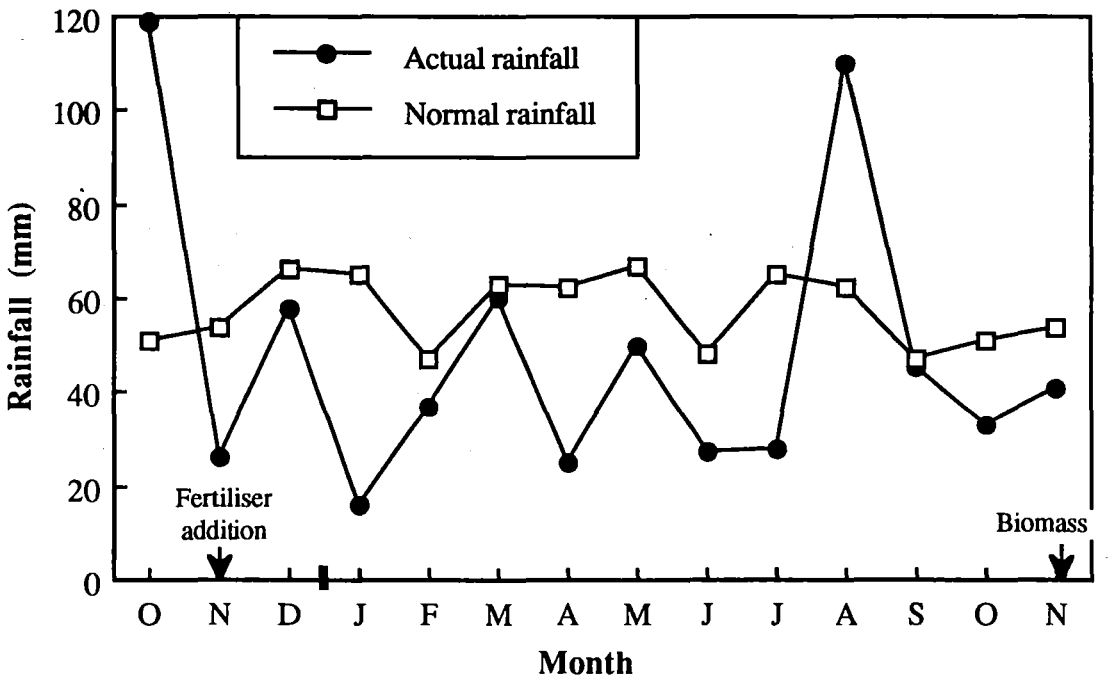


Figure 5.2: Actual and normal monthly rainfall from October 1989 to November 1990 at Rangiora, Canterbury.

5.3.2 Soils

At the time of the Ashley biomass sampling, soil samples were taken to give an indication of the nutritional status of the site and to measure the residual levels of the N and B fertilisers in the soil.

The soils at Ashley Forest were strongly acidic with a pH of around 5. The addition of N (**Figure 5.3**) had a significant effect ($p<.001$) in reducing soil pH. Lowering soil pH is the residual effect of urea (McLaren and Cameron 1990). There was also a significant interaction between N addition and soil depth ($p=.02$). With increasing soil depth the added urea-N had less effect on soil pH levels.

The mean levels of total N% (**Table 5.2**) and mineral N (**Figure 5.4**) declined down the soil profile. Total N% contents ranged from 0.046 to 0.170 and rated very low to low (Blakemore *et al.* 1987). Total N% was not significantly affected by the addition of N. Mineral N represented 2.2 to 4.8% of

total N% and was significantly affected by depth (p=.001). Mineral N levels were higher in the top 20cm of the profile where urea-N had been added. This difference was significant (p<.05) for the 0 to 10cm depth.

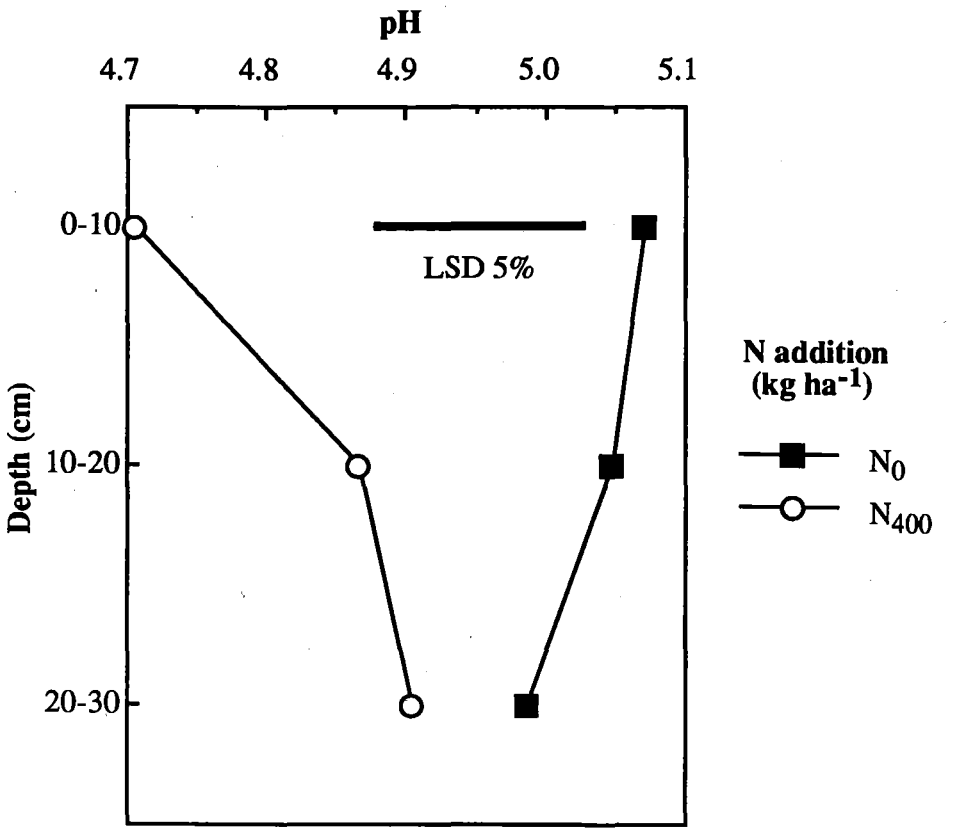


Figure 5.3: Effect of urea-N addition on the pH, to a depth of 30cm, in the soil profile at Ashley Forest.

These results indicate that there was no residual N present in the soil after 1 year. While the amount of mineral N was higher in the upper profile with N addition the overall effect on total N was undetectable as mineral N only represented a small portion of total N. Further investigation of the amount of total N in the whole profile showed that there was no difference between the N_0 and N_{400} average 0 to 30cm total N - both were 0.11%.

The level of organic C in the soil ranged from 0.06 to 3.9% and was significantly affected by depth (p=.004). The mean amounts of organic C% (**Table 5.2**) were very low to low according to the ratings for chemical properties described by Blakemore *et al.* (1987).

The Bray 2 P levels at Ashley were low and ranged from 1.0 to 16.8 $\mu g\ g_{-1}$ for the first extraction. The mean amount of Bray 2 P for each extraction and at each depth are presented in **Table 5.2**. Ballard (1974) recommended P fertiliser applications at planting time for a Bray 2 P (first extraction) value of <12 $\mu g\ g_{-1}$. As P was added as a basal dressing, at 14kg ha^{-1}, to the plots, the natural Bray 2 P levels are likely to be even lower. However, trees at Ashley have not responded to P fertiliser addition in the past (J.A. Adams, pers. comm., 1992) suggesting that the soil is capable of supplying low amounts of P long-term for tree uptake. However, at the time when the trial was put in, it was decided that a low rate of P would be added to the whole trial to avoid any possible problems with low P levels limiting the tree response to the fertiliser applications.

Table 5.2: The mean levels of soil nutrients taken during the Ashley Forest biomass study of radiata pine trees one year after the addition of N and B fertilisers. Apart from Bray 2 P, for each nutrient means followed by the same letter were not significantly different ($p<.05$).

Depth (cm)	Total N%	Organic C%	Bray 2 P ($\mu g\ g^{-1}$)			Bray 2 cations (me%)			
						K	Ca		Mg
			1	2	3		B_0	$B_{7.4}$	
0 to 10	0.133 a	2.6 a	9.4	5.8	3.8	0.26 a	1.5 bc	2.6 a	1.4 a
10 to 20	0.128 a	2.1 ab	4.8	2.3	2.0	0.23 ab	1.2 bc	2.1 ab	1.2 ab
20 to 30	0.077 b	1.5 b	3.6	1.8	1.6	0.19 b	1.1 c	1.0 c	1.1 b

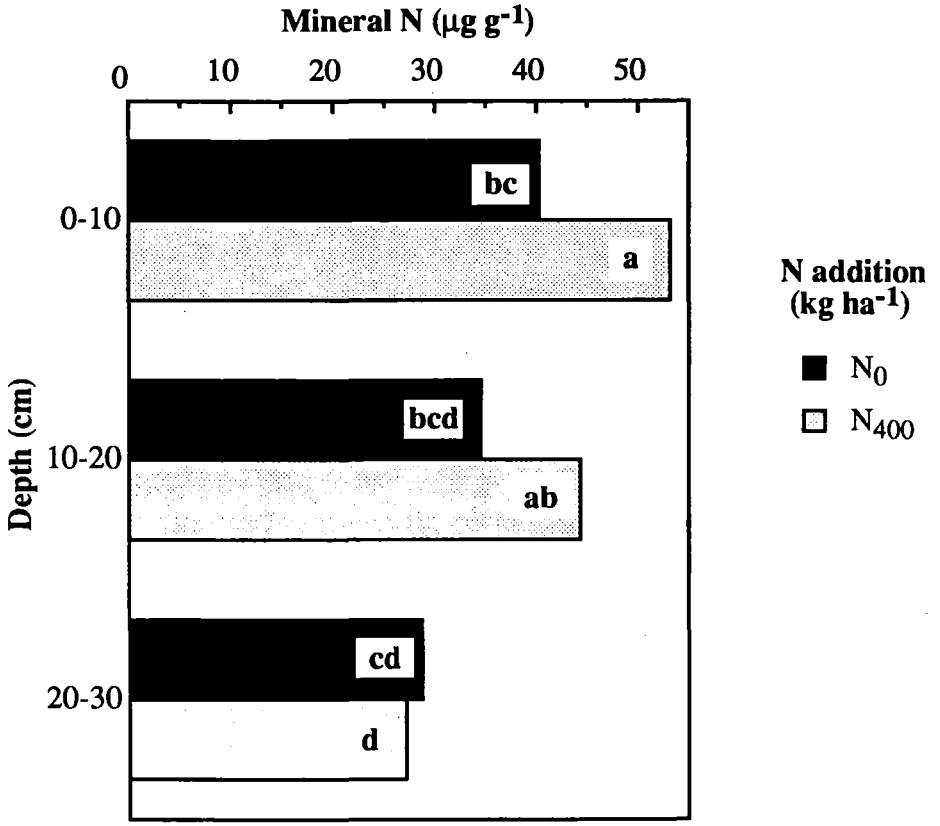


Figure 5.4: Effect of N addition on the average amount of mineral-N in the Ashley Forest soil profile. Means with the same letter were not significantly different ($p<.05$).

The sequential extraction method of Bray 2 P has been used to assess the ability of the soil to supply P with time. Skinner *et al.* (1991) described 4 categories of "available" P extracted with Bray 2 reagent. The Makerikeri hill soil at Ashley appears to be category 2 - although the first Bray 2 extract was less than 12µg P g^{-1} soil, the decline in available P over the three extractions was gradual. These results tend to confirm the soils ability to supply adequate P for tree growth in these soils.

The amounts of Bray 2 K were not significantly affected by N or B fertiliser addition but did vary with increasing soil depth ($p=.066$). With depth the amount of Bray 2 K significantly ($p<.05$) decreased from 0.26me%, at a depth of 0 to 10cm, to 0.19me% at 20 to 30cm (**Table 5.2**). In

contrast, Bray 2 Ca was significantly affected by B addition (p=.029) and depth (p=.022). The amount of Ca was higher where B had been added - this result could be expected as ulexite contains 10% Ca. The amount of Bray 2 Ca was significantly higher in the 0 to 10cm depth with $B_{7.4}$ addition (**Table 5.1**). With increasing depth the amount of Bray 2 Ca declined.

Bray 2 Mg levels were significantly affected by N (p<.001) and B (p=.02) additions and soil depth (p=.030). There was also a significant interaction between N and B (p<.001). Generally the amount of Bray 2 Mg declined with increasing soil depth (**Table 5.2**). Bray 2 Mg amounts were highest in the control plots (**Figure 5.5**) and lowest for $N_{400}B_0$. The addition of $B_{7.4}$ alone also depressed the amount of Bray 2 Mg, compared to the control. When B was added with N - $N_{400}B_{7.4}$ - the resulting amounts of Bray 2 Mg were higher than N alone and not significantly different from $N_0B_{7.4}$. The effect of the fertilisers on Bray 2 Mg was probably indirect and may have reflected the increased demand for Mg by the fertilised trees.

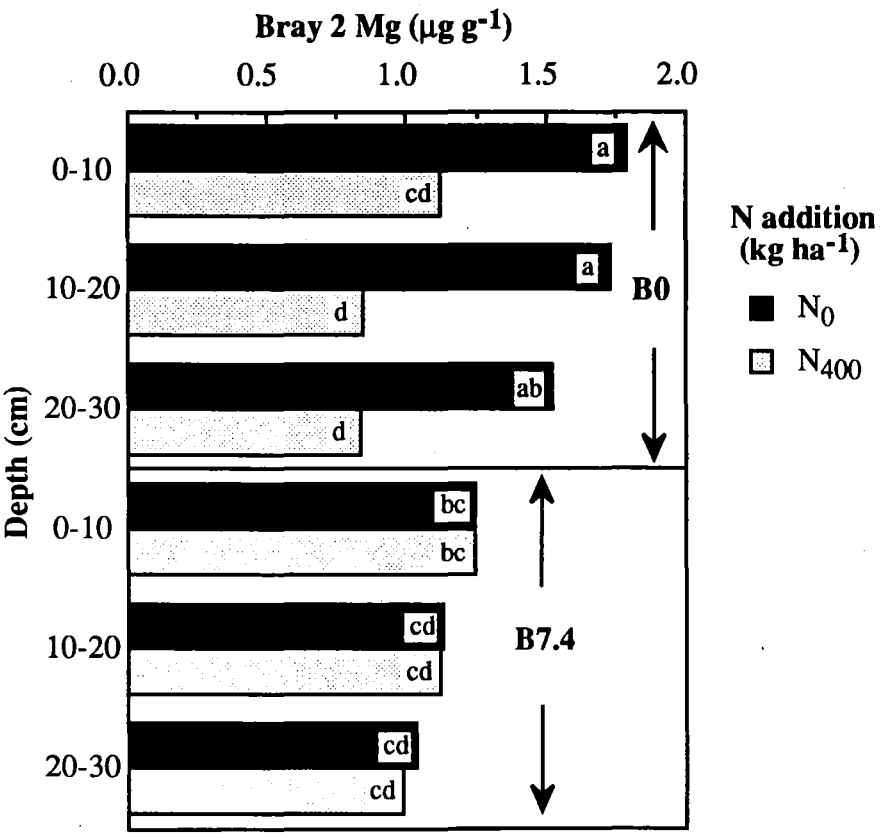


Figure 5.5: Effect of N and B addition and soil depth on the amounts of Bray 2 Mg extracted from the Ashley Forest soil samples. Means with the same letter were not significantly different (p<.05).

The amounts of cations extracted by the Bray 2 method are comparable to the exchangeable cation concentrations found by ammonium acetate leachings (Ballard 1978) and would therefore rate as medium for Mg and very low for Ca and K (Blakemore *et al.* 1987).

The levels of B found by the hot-$CaCl_2$ method were significantly affected (p<.001) by both the application of B, as ulexite, and soil depth and the interaction of these two factors (**Figure 5.6**). B addition greatly increased the amount of B extracted from the 0 to 10cm depth which accentuated the general decrease of hot-$CaCl_2$ B down the profile.

The hot-$CaCl_2$ method extracts very similar amounts of B to the hot-water-soluble method (Adams *et al.* 1991). Using the hot-water-soluble method, Snowdon (1982) found that B deficiencies in radiata seedlings did not occur at levels above 0.35mg B kg^{-1}. The amount of B in the Makerikeri hill soil was greater than 0.35mg B kg^{-1} but the site is considered marginal in the supply of B for radiata pine growth so ulexite is routinely added at 7.4kg B ha^{-1} when the stand is 2 years old.

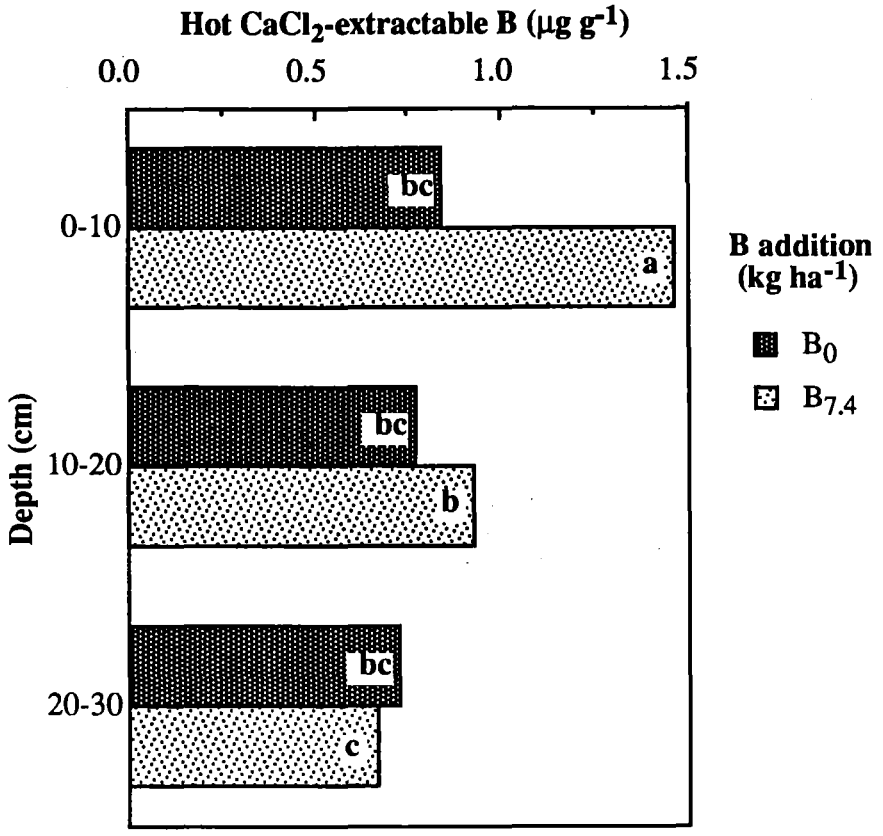


Figure 5.6: Effect of B addition, as ulexite, on the amounts of hot $CaCl_2$-extractable B in the Ashley Forest soils. Means with the same letter were not significantly different ($p<.05$).

Soil B was also extracted using a fractionation scheme (see Chapter 6) and the results (**Table 5.3**) indicated that the amount of B found in the more plant-available non-specifically adsorbed and specifically adsorbed fractions had been significantly increased in the top 20cm by B addition. It is interesting to note that the sum of these two fractions is similar to the amount of B extracted by the hot-$CaCl_2$ method. Correlations between the sum of the two B fractions and hot-$CaCl_2$ B were significant for the 0 to 10cm ($p<.01$) and 10 to 20cm ($p<.1$) increments.

The soil B contents from the 0 to 10cm depth of the third profile (furthest down the slope) in the $N_{400}B_{7.4}$ plot were extremely high and were not included in the ANOVA as they skewed the otherwise normal distribution of the results. The amount of B found in the 0 to 10cm depth by the hot-$CaCl_2$ method was 9.8µg g^{-1} and for the non-specifically adsorbed and specifically adsorbed B fractions 12.4 and 5.4µg g^{-1} respectively. These results indicate that down-slope movement of B could be significant. B movement was not detected in the $N_0B_{7.4}$ plot but this does not discount the possibility of the added B moving beyond the lowest profile sampled in this plot.

Table 5.3: The effect of B addition (added as ulexite 1 year earlier) on the amount of B, measured during a fractionation scheme, down the soil profile at Ashley Forest. Within each fraction, means with the same letter were not significantly different ($p<.05$).

B treatment and depth (cm)		Non-specifically adsorbed	Specifically adsorbed	Amorphous Fe and Al oxide	Crystalline Fe and Al oxide
B_0:	0 to 10	0.33 bc	0.35 b	3.5 ab	4.3 a
	10 to 20	0.22 c	0.22 b	2.9 bc	4.6 a
	20 to 30	0.20 c	0.23 b	2.5 c	4.1 a
$B_{7.4}$:	0 to 10	0.65 a	0.69 a	3.9 a	3.7 a
	10 to 20	0.45 b	0.61 a	3.7 ab	4.2 a
	20 to 30	0.22 c	0.23 b	3.0 abc	4.2 a

It seems possible that a similar fate could have occurred for the added N and could explain why the amount of total N% in the soil was unaffected by urea-N addition. The highest amount of total N, 0.23%, for the 0 to 10cm depth was also measured for the third profile (i.e. furthest down the slope) in the $N_{400}B_{7.4}$ plot. However, it should be noted that the mean total amount of soil N, in those plots not receiving added N, was 1700, 1332 and 744kg ha^{-1} in the 0 to 10, 10 to 20 and 20 to 30cm depths, respectively, assuming a soil bulk density of 1.2g cm^{-3}. The addition of 400kg N ha^{-1} therefore represented about 10% of what was already present in the soil to a depth of 30cm. After N uptake by the trees and particularly the weeds, the residual N may be difficult to measure given the possible errors associated with sampling and chemical analysis. The soil samples were taken from the pit dug to remove the tree stump. This volume of soil may have been more fully explored by the tree roots so that the readily available inorganic N from the fertiliser may have been quickly removed from the soil and thus no residual N was identified in the total N% values.

Generally, there was a lot of soil variability associated with the site. The amounts of organic C, total and mineral N and Bray 2 cations increased or fluctuated down some of the profiles. Such differences were most likely a result of the soil disturbance which occurred during site clearing and the windrowing of debris after the harvest of the first rotation. It appeared that some profiles had been partially or completely inverted with possible mixing of the horizons. Soil depth was, however, still an important factor in describing nutrient changes within the soil profile and the average amounts of the measured nutrients generally decreased with increasing depth.

The soil results confirm that the Ashley Forest site was nutritionally marginal for radiata growth and, as such, was ideal for investigating the effect of fertiliser additions - the tree response would be apparent externally as increased growth and internally through changes in nutrient concentrations.

Evidence of the fertiliser additions to the soil was present 1 year later, particularly for B. The added N and/or B also affected other soil nutrient levels, such as Bray 2 Ca and Mg, and the pH of the soil.

5.3.3 Tree growth

The average total above-ground dry weight of the fertilised trees was significantly greater than the control trees (**Figure 5.7**). The average control tree had a dry weight of 1.6kg compared to 3.7kg where $B_{7.4}$ had been added alone or with N. The $N_{400}B_0$ tree had an average dry weight of 3.0kg.

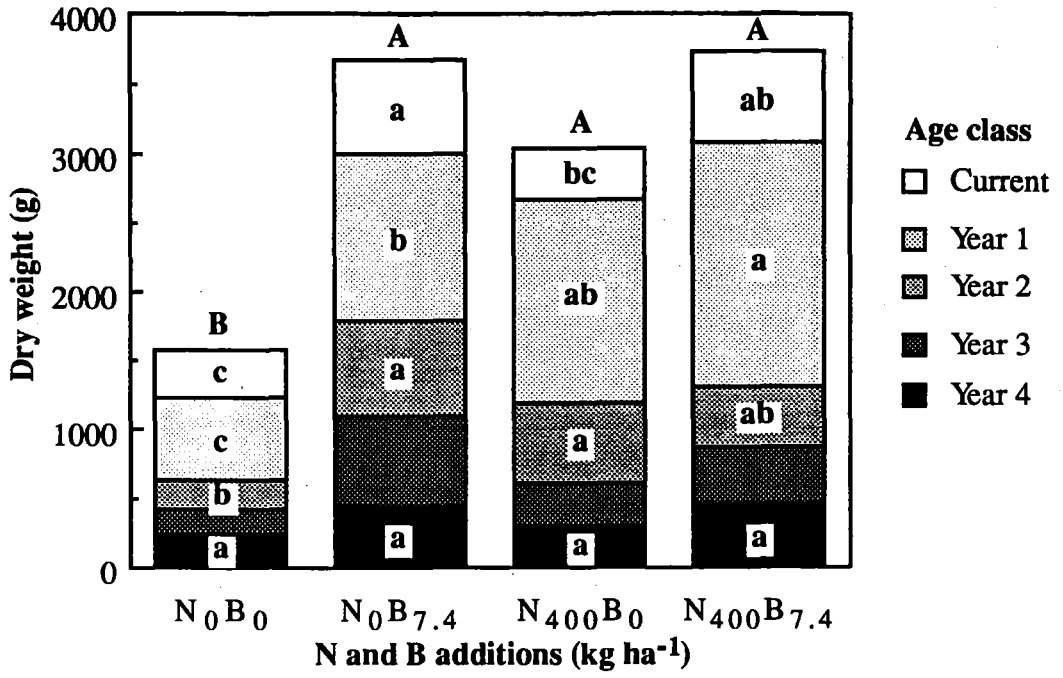


Figure 5.7: Effect of N and B fertiliser addition on dry weights of age classes of the above-ground biomass portion of radiata pine at Ashley Forest. Age class and total dry weight means with the same letter were not significantly different ($p<.05$). Raw data for Year 3 was skewed, therefore the means have not been differentiated by a least significant difference.

The greatest proportion of the above-ground biomass was current or 1 year-old growth - from 51% for $N_0B_{7.4}$ to 65% for $N_{400}B_{7.4}$ (**Figure 5.7**). When the fertilisers were added alone (i.e. $N_0B_{7.4}$ and $N_{400}B_0$) they had a similar effect on the amount of current and 1 year-old dry matter produced (**Figure 5.8**). However the dry matter distribution between the current and 1 year-old components was different.

The addition of N significantly affected the current ($p=.051$), 1 year-old ($p=.077$) and 2 year-old ($p=.038$) stem and the 1 year-old ($p=.063$) and 2 year-old ($p=.020$) bark. The weights of these components (except the current stem) were higher with the addition of N400 particularly in the $N_{400}B_0$ treatment (**Appendix 2a**). The addition of B was significant for the current ($p=.012$) and 1 year-old needles ($p<.001$) and the current ($p<.025$) and 1 year-old ($p=.025$) branches. The addition of B increased the weight of these components.

The average weight of the 1 year-old needles from radiata pine trees that had received N400 was 937g which was significantly ($p<.05$) higher than the 501g for the control. However, N addition did not significantly affect the weight of the current needles (**Appendix 2a**). These results suggest that the effect of N addition in promoting needle growth was short lived and essentially restricted to the 1 year-old needles. However, the addition of B still significantly affected the current needles and stem.

The only negative effect of fertiliser addition on tree dry weights occurred for the addition of N on the current stem. The $N_{400}B_0$ current stem weight of 7.6g was much lower than the 19.2g for the control treatment (**Figure 5.9**). This difference was not significant. The effect of N on the current stem was in direct contrast to the positive effect it had on the dry weight of the 1 year-old stem. It has been shown that fertilisers added to radiata pine without irrigation during a dry summer can result in lower volume increments than for unfertilised trees (Linder 1987).

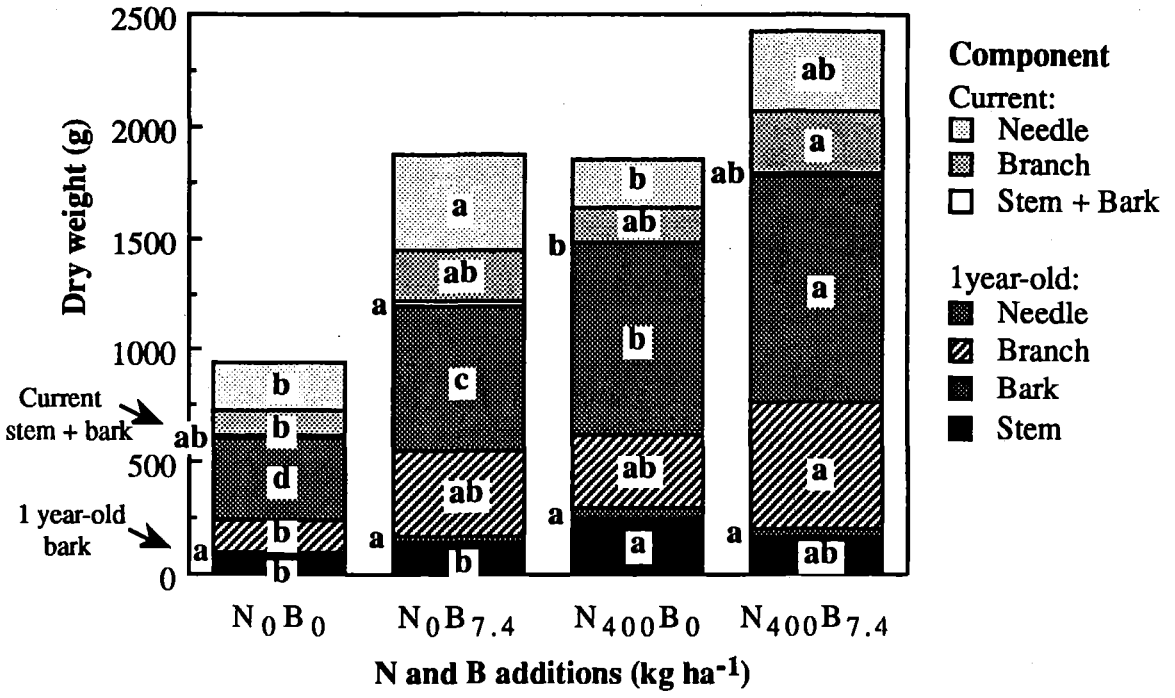


Figure 5.8: Effect of the N and B fertiliser additions on the dry weights of the current and 1 year-old radiata pine tree components at Ashley Forest. Components with the same letter were not significantly different ($p<.05$).

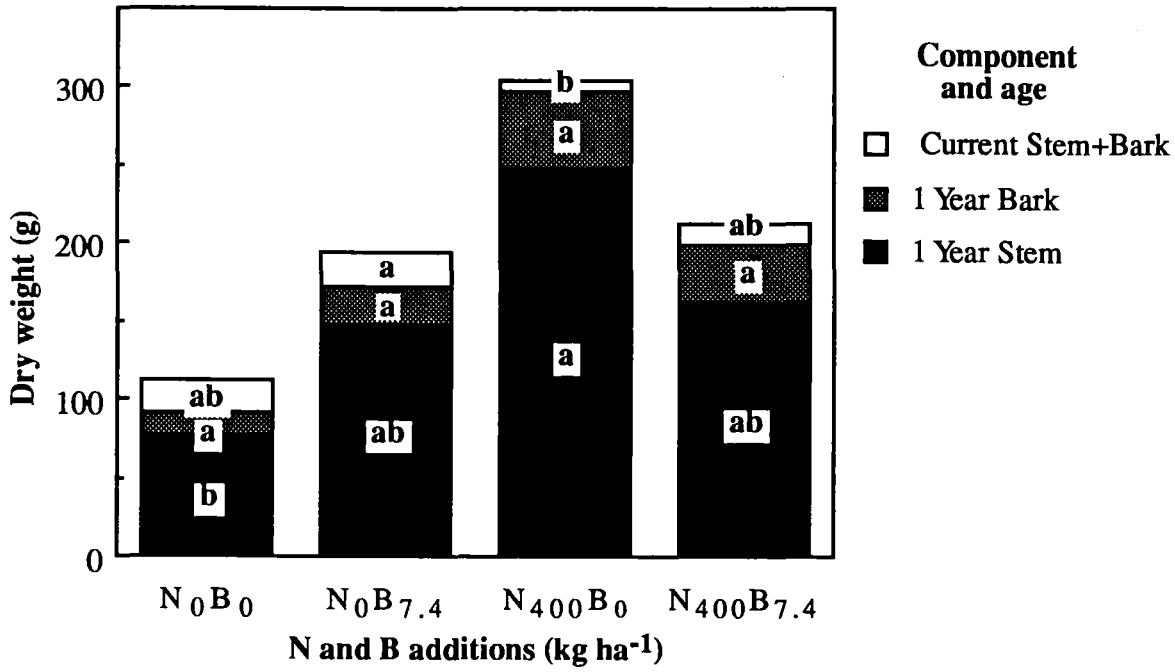


Figure 5.9: Effect of N and B fertiliser addition on the dry weights of the current stem and 1 year-old stem and bark of young radiata pine at Ashley Forest. For each component, means with the same letter were not significantly different ($p<.05$).

Within the age classes, different tree components dominated the above-ground biomass - from the stem, which was 82% of the 4 year-old weight, to the needles which represented 59% of the current tree weight and 57% of the 1 year-old tree weight. It should be noted that the 4-year-old stem contained all ages of wood.

Overall, the needles represented the greatest portion of the average above-ground tree dry weight (39%) followed by the stem (32%), branches (24%), and bark (5%). As the weight of foliage in young trees can represent 60 to 70% of the total biomass there are large reserves of nutrients which can be cycled internally to support growth (Nambiar 1990). The dominance of the needle component is important for young plantations where the amount of litterfall is low.

The fertiliser additions had an effect on the allocation of tree biomass into the different component portions. Those trees sampled from plots where B had been added had a higher proportion of branches, at 26%, compared to 21% where no B was added. In trees from the $N_{400}B_{7.4}$ plot the proportionate contribution of stem to the total dry weight was less at 27% compared to the 33 to 34% for the other sampled plots. These differences may not be directly related to the fertiliser treatments as the components also contained the older aged portions.

The addition of B had a positive and significant (p=.053) effect on the dry weight of the stump with an average of 308g compared to 225g where no B was added.

The older-age needles were the only other tree components that appeared to be significantly (p<.05) affected by B fertiliser addition (**Figure 5.10**). Overall the total 2 to 4 year-old needle dry weights ranged from 63g for N_0B_0 to 255g for $N_0B_{7.4}$. The average older-age needle dry weights were greater where B had been added. But were these differences a function of the fertiliser additions? Knight (1978) described mature foliage as that which developed during the spring and summer and was sampled in the autumn. This suggests that the 2 to 4 year-old needles would have been 1 to 3 year-old needles at the time of the fertiliser application and already mature and should not have increased their weight in response to the addition of fertilisers. The dry weight differences recorded in this study may therefore reflect a difference in average plot tree size (weight) before the fertiliser addition. If such differences existed, they may have been a result of soil chemical and/or physical variability within the block sampled, a difference in the planting stock or an unfortunate random sampling of the trees which has exaggerated the effect of the fertilisers, particularly B, on tree growth.

It is also possible that needles may have been lost by the unfertilised trees. Linder (1987) found that fertilised 11 to 12 year-old radiata pine tended to have reduced leaf shedding during a wet summer, compared with non-fertilised trees, but similar amounts of leaf shedding during a summer drought. Linder and Rook (1984) recognised the importance of other factors such as light, water and pathogens which affect leaf retention. They also suggested that for trees growing in open conditions an increase in nutrient supply may increase leaf longevity. In contrast, Will and Hodgkiss (1977) found that increasing the supply of N and P, to open-grown radiata pine, decreased leaf longevity although considerably larger quantities of foliage were produced each year. Burdon (1976) found no clear relationship between radiata pine needle nutrition and retention except that foliage was retained much longer at drier sites with no evident nutrient deficiencies.

Thus the reasons behind the larger needle weights in the fertilised trees, particularly $N_0B_{7.4}$, are difficult to determine but could be a result of needle loss by the control trees or a disparity in tree size prior to the fertiliser addition.

Separately, the two fertilisers increased the weight of the above-ground tree - particularly B. Where the fertilisers were added together there was no additional biomass production above the $N_0B_{7.4}$ level. The fertilisers generally promoted the growth of different tree components. Both fertilisers promoted the production of 1 year-old needles but only B enhanced current needle production above the control

level. This short term response of the trees to N fertilisers has been noted before. Knight *et al.* (1983) found that the response of 4 to 5 year-old radiata pine diameter increment and foliar N% to N addition lasted about 1 year. In contrast, response of foliage B concentrations to B fertiliser addition persisted for 5 years.

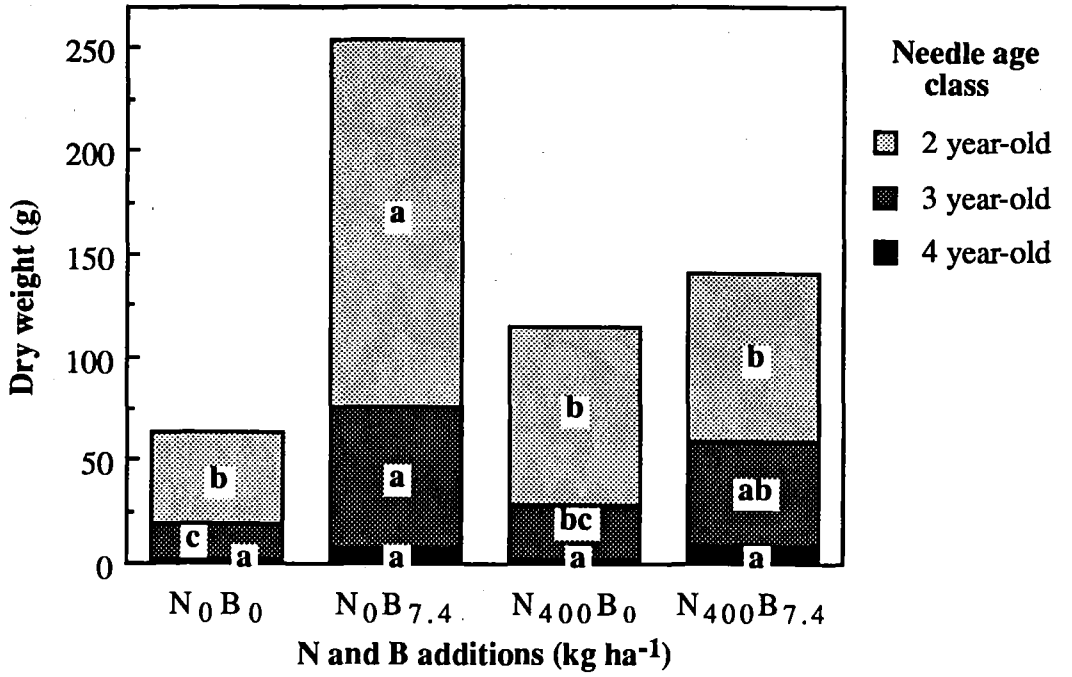


Figure 5.10: Effect of N and B fertiliser addition on average dry weights of the older-aged needles of radiata pine at Ashley Forest. For each age class, means with the same letter were not significantly different ($p<.05$).

5.3.4 Nutrient concentration changes within the tree

5.3.4.1 Above-ground tree

Although the fertiliser additions had a large effect on the growth of the trees it is difficult to describe this in terms of nutrient uptake within the sampled age classes of wood. Because of the way these trees were sampled, the branch and stem age classes actually represented a varying range of wood ages (**Figure 5.11**). As the effect of the fertilisers on nutrient concentrations in this trial included dilution, retranslocation and storage, differentiating between these effects when a range of age classes were present was difficult. In general, an overall change in nutrient concentrations in a section of wood could represent a large change in one or more of the age classes. The more recent the branch or stem the greater the proportion of current and 1 year-old age classes and the more likely a change due to fertiliser addition through dilution and/or storage. For the older age classes, changes in nutrient concentrations could be via retranslocation and/or storage.

The changes in the amounts of nutrient within a component indicate whether changes in nutrient concentrations were due to dilution, retranslocation and storage. If dilution occurs, the amounts of nutrient in a component should remain the same while for retranslocation the amount of the nutrient should decrease. Storage of a nutrient would result in an increase in its concentration and amount within a component. These processes may also occur simultaneously so that the observed value will represent the net effect.

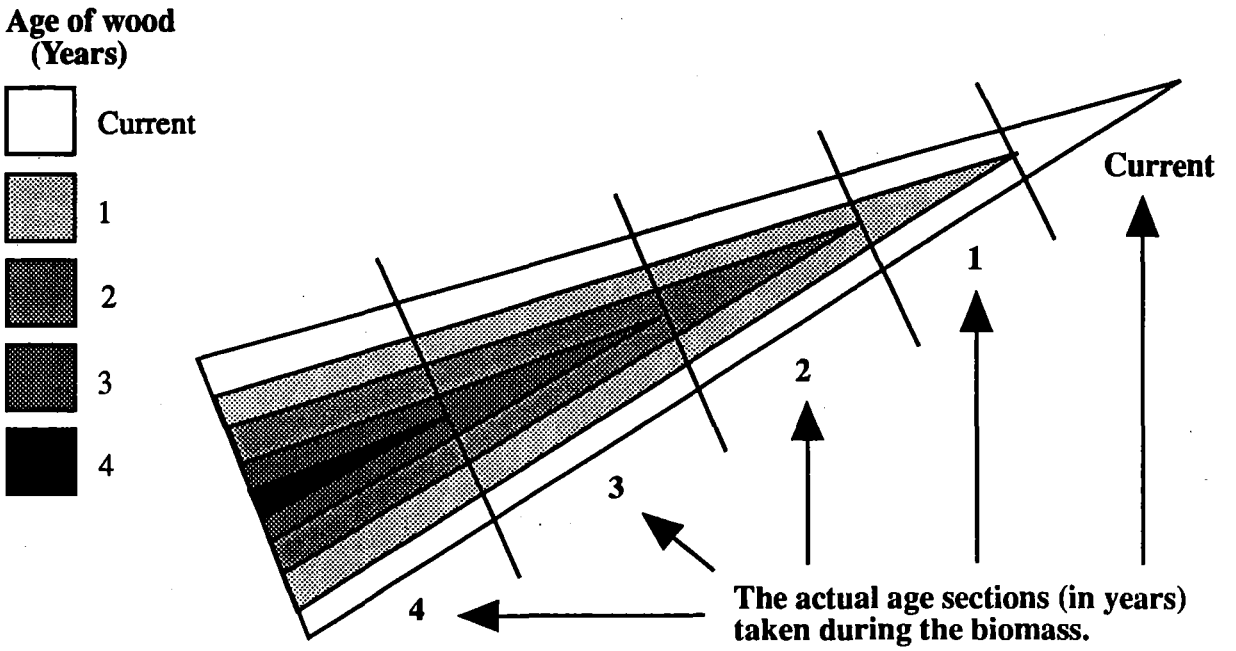


Figure 5.11: The different age classes of wood present in a radiata pine stem or branch and the sections taken during the biomass at Ashley Forest.

The concentrations of K, Ca, Cu and Zn throughout the trees were the least affected by fertiliser additions (**Tables 5.4c, 5.4d, 5.4f and 5.4g** respectively).

For K, the significant fertiliser effects were negative. The K% of the 1-4 year-old stem in the fertilised treatments were significantly ($p<.05$) lower than the control. The stem may therefore represent a source of retranslocatable K or concentrations may have decreased as a result of dilution.

There were no significant fertiliser effects on the Ca concentrations of any of the tree components. Generally, the highest Ca% for most components were recorded for the $N_{400}B_{7.4}$ treatment - particularly in the branches, stem and bark - and the lowest for the control.

Copper concentrations were significantly lower than the control in the 2 to 4 year-old stem where $B_{7.4}$ had been added alone or with N. Generally the concentrations were higher in the $N_{400}B_0$ trees. As with K, the significant effect of B addition was negative and the older stem appeared to be a source of retranslocatable Cu or concentrations were diluted..

The concentrations of Zn in the fertilised tree components were lower than in the control. This effect was significant for a variety of components in the $N_0B_{7.4}$ trees - the 2 to 4 year-old branches, all ages of bark and the 1 and 3 year-old stem. As the needle concentrations in these trees were not significantly lower than the control it may be that the above components were a source of retranslocatable Zn or concentrations had been diluted.

Generally N concentrations were not significantly ($p<.05$) greater where urea-N had been added compared to the control plots (**Table 5.4a**). Of the two N treatments $N_{400}B_0$ produced a greater response in N concentrations than did $N_{400}B_{7.4}$. The components in the $N_{400}B_0$ trees that had significantly higher N% included 4 year-old needles, 4 year-old bark and the smaller roots. For the older age components, the presence of added N may have reduced the trees requirement to retranslocate N. Where B had been added alone ($N_0B_{7.4}$) the N concentrations were significantly

($p<.05$) lower than the control for some tree components (e.g. current branches and 1 year-old needles and stem). This indicated that N uptake did not maintain N concentrations for the greater growth exhibited by the $N_0B_{7.4}$ trees possibly resulting in the dilution of N concentrations within the younger tree components (e.g. 1 year needles and the current branches) and retranslocation from older tree components (e.g. 4 year needles and 2-4 year-old stem). Even where N was added alone, stem components had N% levels significantly less than the control.

B addition, as ulexite, greatly enhanced B concentrations compared to the control and $N_{400}B_0$ treatments (**Table 5.4h**). Those components with significantly ($p<.05$) higher B concentrations included all age classes of needles, current and 1 year-old branches, current stem, all ages of bark and roots. B concentrations were generally higher where B had been added alone (i.e. $N_0B_{7.4}$) than where N and B were added together.

Stone (1990) stated that generally B concentrations in twigs and stem bark were much less than in the foliage but greater than in the stem wood. **Table 5.4b** shows that the B concentrations in the branches and stem bark were quite high, particularly in the stem bark, and greater than the B concentrations in the needles where no B had been added.

Within the tree the concentrations of P (**Table 5.4b**), and to a lesser extent Mg (**Table 5.4e**), were reduced by N and/or B fertiliser addition. Many of the tree components receiving the $N_{400}B_{7.4}$ treatment had P concentrations significantly lower than the control - particularly in the needles and the stem. All three fertiliser treatments resulted in Mg concentrations significantly less than the control in the branches, stem, bark and the smallest roots. The concentrations of Mg in the needles were relatively unaffected by the fertiliser additions suggesting that Mg was retranslocated to maintain needle concentrations and that the older needles were not a source of retranslocatable Mg.

The relative concentration of nutrients in the tree components usually decrease in order of: foliage, stem bark, live branches, stem wood (Madgwick *et al.* 1977). In this study the order was essentially the same except that the ranking for the stem bark and branch depended on the nutrient. Within the age classes of stem bark from 1 to 4 year-old, nutrient concentrations remained relatively constant with Ca, Mg, Cu, Zn and B slightly increasing while N, P and K decreased. However, in the branches the change in nutrient concentrations from current to 4 year-old also depended on the nutrient. The concentrations of N, P and K substantially decreased while Ca increased. Because of these concentration changes in the branches and stem bark, there were instances where nutrient concentrations, particularly in the current branch, exceeded those found in the bark (e.g. P and K).

Nutrients differ greatly in their mobility in plants - the ease with which they can be physiologically moved (Attiwill and Leeper 1987). The concentrations of mobile elements such as N, P, and K declined in the needle with increasing needle age (Madgwick *et al.* 1988a) while Ca and Zn concentrations increased (Madgwick *et al.* 1977). Madgwick *et al.* (1977) found no consistent trend for P and Mg concentrations.

Even within one age class nutrient concentrations vary depending on their sampling position within the crown. For instance, Cromer *et al.* (1985b) found a decrease in the concentrations of N, P, K from the top to the base of the green crown within 1 age class of needles from 10 year old radiata pine.

According to Madgwick *et al.* (1977) nutrient concentrations tend to decline in the stem and branch with increasing tree age (except for Ca).

These trends in nutrient concentration changes with age were confirmed in this biomass study. In the needles the concentrations of N, K and Cu declined with age while Ca, Mg and Zn increased. The concentrations of P fluctuated with needle age while B concentrations were fairly similar. In the branches nutrient concentrations declined except for Ca and Mg whose concentrations remained relatively stable. Only Ca concentrations increased with increasing stem wood age while in the stem bark the nutrient concentrations stayed relatively constant with age.

5.3.4.2 Below-ground tree

The stump tended to have higher nutrient concentrations than the stem (**Tables 5.4a to 5.4h**) suggesting that it may be a nutrient storage area prior to nutrient transport into the above-ground components. The nutrient concentrations within the stump were significantly affected by fertiliser addition compared to the control - Cu concentrations were significantly lower with $N_{400}B_{7.4}$ while N and Mg were significantly lower with $N_0B_{7.4}$.

Within the three root categories the finest roots (i.e. <0.25cm) had higher nutrient concentrations and were more likely to be affected by fertiliser addition (**Tables 5.4a to 5.4h**). Compared to the control, the significant effect of fertiliser addition depended on the nutrient and the root category (**Table 5.5**).

The lower concentrations of nutrients (e.g N, K, Mg and Cu) in the fine roots of the fertilised trees may reflect the exhausting of immediate soil reserves by the fertilised trees or less nutrient storage in the roots by those trees with a high demand for certain nutrients.

5.3.5 General discussion

It is difficult to assess the importance of nutrient concentration changes throughout the different age and type of tree components as a result of the fertiliser additions. The needles represent the 'power house' of the tree and the roots the point of nutrient uptake - changes that affect the growth of these components, particularly the youngest in age, may greatly affect further tree development. The other tree components - stem, branches, older needles etc. - from a nutrient perspective may simply be acting as a storage for excess nutrient uptake (e.g B) and a source of retranslocatable nutrients where nutrient uptake from the soil does not meet the tree demand. Thus the changes in nutrient concentrations of these 'storage areas' may not be important to the overall tree growth and health unless the amount of retranslocatable nutrients is depleted.

Boron fertiliser addition had a greater effect on nutrient concentrations than N addition. The significant effects of added B were positive for B concentrations (i.e. increased B concentrations) and negative for the concentrations of other nutrients. This same trend occurred for the added N - the significant affects were positive for N concentrations and negative for other nutrient concentrations. As the significant fertiliser effects on the dry weights of the tree components were positive one could conclude that the negative effect on the nutrient concentrations were a result of dilution and/or retranslocation. On this site retranslocation may be an important mechanism to ensure sufficient nutrient concentrations in the youngest tree components - especially where fertilisers promoted tree growth.

Table 5.4: Effect of N and B fertiliser addition on the nutrient concentrations of the radiata pine biomass components at Ashley Forest. For each component, means with the same letter were not significantly different ($p<.05$). The distribution of data from components marked with an '*' was skewed and no further statistics were carried out on the means.

a) Nitrogen (%)

Component	N_0B_0	$N_0B_{7.4}$	$N_{400}B_0$	$N_{400}B_{7.4}$	CV%
Current Needles	1.92 ab	1.69 b	2.00 a	1.82 ab	8.2
1 Year Needles	1.63 a	1.40 b	1.67 a	1.49 ab	6.1
2 Year Needles	1.30 a	1.11 a	1.33 a	1.23 a	13.8
3 Year Needles	1.26 a	1.04 a	1.34 a	1.23 a	15.9
4 Year Needles	1.01 b	0.82 c	1.18 a	1.07 ab	8.0
Current Branch	1.07 a	0.88 b	1.19 a	1.06 a	7.9
1 Year Branch	0.50 a	0.48 a	0.58 a	0.47 a	14.9
2 Year Branch	0.36 ab	0.29 b	0.32 ab	0.42 a	19.3
3 Year Branch	0.27 ab	0.20 b	0.25 a	0.29 a	17.6
4 Year Branch	0.25 a	0.20 a	0.27 a	0.25 a	13.1
Current Stem	1.06 ab	0.75 b	1.16 a	0.92 ab	16.8
1 Year Stem	0.231 a	0.157 b	0.178 b	0.203 a	6.5
2 Year Stem	0.196 a	0.151 b	0.148 b	0.148 b	10.3
3 Year Stem	0.159 a	0.108 b	0.144 ab	0.153 a	13.6
4 Year Stem	0.155 a	0.122 b	0.129 b	0.154 a	8.1
1 Year Bark	0.74 a	0.64 a	0.81 a	0.72 a	15.1
2 Year Bark	0.66 a	0.56 b	0.73 a	0.71 a	7.3
3 Year Bark	0.61 b	0.54 c	0.68 a	0.69 a	5.7
4 Year Bark	0.57 ab	0.45 b	0.67 a	0.67 a	15.5
Stump	0.340 a	0.198 b	0.298 a	0.355 a	16.4
Roots (>1cm)*	0.25 a	0.26 a	0.29 a	0.30 a	18.4
Roots (0.25 - 1cm)	0.35 b	0.38 b	0.55 a	0.48 ab	15.7
Roots (<0.25cm)	0.62 bc	0.49 c	0.83 a	0.65 b	13.4

* Sizing refers to root diameter.

5.4 b) Phosphorus (%)

Component	N_0B_0	$N_0B_{7.4}$	$N_{400}B_0$	$N_{400}B_{7.4}$	CV%
Current Needles	0.31 a	0.31 a	0.23 b	0.19 b	12.9
1 Year Needles	0.169 a	0.169 a	0.171 a	0.155 a	18.4
2 Year Needles	0.122 b	0.154 a	0.112 bc	0.105 c	6.5
3 Year Needles*	0.141	0.135	0.114	0.169	21.9
4 Year Needle*	0.273	0.141	0.116	0.120	9.7
Current Branch	0.185 ab	0.211 a	0.156 bc	0.131 c	13.4
1 Year Branch	0.097 a	0.094 a	0.078 a	0.083 a	13.9
2 Year Branch	0.060 a	0.059 a	0.047 a	0.050 a	13.4
3 Year Branch	0.091 ab	0.051 bc	0.105 a	0.042 c	30.7
4 Year Branch*	0.043	0.043	0.122	0.039	80.9
Current Stem	0.177 ab	0.218 a	0.133 b	0.146 b	17.4
1 Year Stem	0.062 a	0.060 a	0.037 c	0.049 b	9.6
2 Year Stem	0.058 a	0.038 b	0.040 b	0.042 b	14.6
3 Year Stem	0.031 a	0.035 a	0.032 a	0.019 b	18.2
4 Year Stem	0.041 a	0.044 a	0.049 a	0.036 a	36.8
1 Year Bark	0.112 ab	0.119 ab	0.096 b	0.141 a	14.1
2 Year Bark	0.124 a	0.107 ab	0.112 ab	0.091 b	10.8
3 Year Bark	0.126 a	0.109 ab	0.107 ab	0.104 b	10.0
4 Year Bark*	0.106	0.109	0.094	0.168	38.1
Stump	0.080 ab	0.082 ab	0.091 a	0.072 b	7.6
Roots (>1cm)	0.084 a	0.119 a	0.104 a	0.122 a	28.9
Roots (0.25 - 1cm)	0.129 ab	0.158 a	0.090 b	0.102 b	21.3
Roots (<0.25cm)	0.095 a	0.099 a	0.080 a	0.079 a	22.5

5.4 c) Potassium (%)

Component	N_0B_0	$N_0B_{7.4}$	$N_{400}B_0$	$N_{400}B_{7.4}$	CV%
Current Needles	1.18 a	1.12 a	1.07 a	1.04 a	10.5
1 Year Needles	0.67 a	0.76 a	0.49 a	0.68 a	22.7
2 Year Needles	0.78 a	0.75 a	0.44 a	0.71 a	32.6
3 Year Needles	0.53 a	0.75 a	0.32 a	0.58 a	51.5
4 Year Needles	0.40 a	0.60 a	0.27 a	0.60 a	49.7
Current Branch	1.41 a	1.34 a	1.22 a	1.02 a	17.0
1 Year Branch	0.56 a	0.60 a	0.56 a	0.46 a	16.7
2 Year Branch	0.34 a	0.34 a	0.28 a	0.33 a	19.1
3 Year Branch	0.23 a	0.18 a	0.15 a	0.18 a	23.6
4 Year Branch	0.159 a	0.151 a	0.167 a	0.139 a	23.3
Current Stem	1.05 a	1.34 a	0.85 a	0.87 a	37.6
1 Year Stem	0.32 a	0.28 a	0.177 b	0.20 b	13.9
2 Year Stem	0.22 a	0.153 b	0.126 b	0.115 b	14.8
3 Year Stem	0.18 a	0.118 b	0.116 b	0.098 b	12.6
4 Year Stem	0.165 a	0.119 b	0.090 b	0.098 b	21.3
1 Year Bark	0.53 a	0.47 a	0.34 a	0.38 a	32.9
2 Year Bark	0.40 a	0.38 a	0.33 a	0.22 b	23.5
3 Year Bark	0.35 ab	0.37 a	0.29 abc	0.22 c	19.3
4 Year Bark	0.38 ab	0.34 a	0.30 ab	0.21 b	23.5
Stump	0.27 a	0.22 a	0.22 a	0.26 a	18.8
Roots (>1cm)	0.25 a	0.18 a	0.20 a	0.15 a	32.2
Roots (0.25 - 1cm)	0.34 a	0.39 a	0.32 a	0.23 a	31.5
Roots (<0.25cm)	0.43 a	0.41 ab	0.28 c	0.32 b	17.5

5.4 d) Calcium (%)

Component	N_0B_0	$N_0B_{7.4}$	$N_{400}B_0$	$N_{400}B_{7.4}$	CV%
Current Needles	0.20 a	0.24 a	0.25 a	0.21 a	22.5
1 Year Needles	0.38 a	0.42 a	0.35 a	0.36 a	16.7
2 Year Needles	0.43 a	0.53 a	0.57 a	0.46 a	31.4
3 Year Needles	0.58 a	0.71 a	0.75 a	0.73 a	32.5
4 Year Needles	0.85 a	0.87 a	0.80 a	0.87 a	33.4
Current Branch	0.105 a	0.120 a	0.127 a	0.148 a	18.8
1 Year Branch	0.149 a	0.185 a	0.188 a	0.204 a	17.0
2 Year Branch	0.172 a	0.196 a	0.206 a	0.274 a	24.3
3 Year Branch	0.168 a	0.187 a	0.173 a	0.214 a	19.4
4 Year Branch	0.164 a	0.204 a	0.210 a	0.207 a	29.6
Current Stem	0.084 a	0.087 a	0.080 a	0.114 a	39.6
1 Year Stem	0.056 a	0.048 a	0.060 a	0.069 a	18.4
2 Year Stem	0.058 a	0.058 a	0.059 a	0.070 a	17.5
3 Year Stem	0.062 ab	0.059 b	0.059 b	0.077 a	13.2
4 Year Stem	0.062 a	0.063 a	0.057 a	0.075 a	20.0
1 Year Bark[a]	0.164	0.151	0.157	0.239	27.1
2 Year Bark	0.175 a	0.187 a	0.188 a	0.234 a	23.4
3 Year Bark	0.188 a	0.192 a	0.191 a	0.247 a	23.1
4 Year Bark	0.181 a	0.204 a	0.233 a	0.271 a	32.3
Stump	0.096 a	0.081 a	0.102 a	0.107 a	20.4
Roots (>1cm)	0.084 a	0.081 a	0.088 a	0.091 a	12.1
Roots (0.25 - 1cm)	0.096 a	0.124 a	0.106 a	0.104 a	14.2
Roots (<0.25cm)	0.146 a	0.175 a	0.155 a	0.181 a	13.8

5.4 e) Magnesium (%)

Component	N_0B_0	$N_0B_{7.4}$	$N_{400}B_0$	$N_{400}B_{7.4}$	CV%
Current Needles	0.167 ab	0.153 ab	0.173 a	0.129 b	13.9
1 Year Needles	0.180 a	0.153 a	0.156 a	0.132 a	16.9
2 Year Needles	0.169 a	0.167 a	0.182 a	0.136 a	24.0
3 Year Needles	0.194 a	0.188 a	0.204 a	0.190 a	26.5
4 Year Needles	0.228 a	0.194 a	0.204 a	0.193 a	25.6
Current Branch	0.136 a	0.110 a	0.130 a	0.102 a	16.9
1 Year Branch	0.149 a	0.124 ab	0.146 a	0.117 b	10.0
2 Year Branch	0.157 a	0.111 c	0.127 bc	0.133 b	8.3
3 Year Branch	0.131 a	0.089 b	0.102 b	0.100 b	13.9
4 Year Branch	0.111 a	0.093 a	0.118 a	0.091 a	17.4
Current Stem	0.130 a	0.094 ab	0.097 ab	0.085 b	20.0
1 Year Stem	0.061 a	0.044 b	0.045 b	0.051 ab	13.5
2 Year Stem	0.054 a	0.038 b	0.041 b	0.043 b	13.6
3 Year Stem	0.050 a	0.033 c	0.037 bc	0.044 ab	12.3
4 Year Stem	0.048 a	0.036 b	0.034 b	0.041 ab	14.6
1 Year Bark	0.125 a	0.089 b	0.095 b	0.092 b	10.2
2 Year Bark	0.126 a	0.088 b	0.112 ab	0.098 ab	14.7
3 Year Bark	0.135 a	0.084 b	0.103 b	0.100 b	10.0
4 Year Bark	0.130 a	0.089 b	0.110 ab	0.097 b	13.7
Stump	0.071 a	0.048 c	0.066 ab	0.054 abc	15.7
Roots (>1cm)	0.088 a	0.071 a	0.085 a	0.075 a	14.9
Roots (0.25 - 1cm)	0.126 a	0.128 a	0.129 a	0.099 a	16.7
Roots (<0.25cm)	0.154 a	0.115 b	0.120 b	0.099 b	11.6

5.4 f) Copper ($\mu g\ g^{-1}$)

Component	N_0B_0	$N_0B_{7.4}$	$N_{400}B_0$	$N_{400}B_{7.4}$	CV%
Current Needles	6.0 ab	5.4 b	7.6 a	5.6 b	16.2
1 Year Needles	4.9 a	4.1 a	5.1 a	4.0 a	16.8
2 Year Needles	2.9 a	2.6 a	3.4 a	2.7 a	14.4
3 Year Needles	4.1 a	2.8 b	3.6 ab	3.6 ab	17.6
4 Year Needles	3.5 a	2.9 a	3.9 a	3.1 a	15.5
Current Branch	6.1 ab	5.1 b	8.0 a	5.9 ab	18.2
1 Year Branch	4.7 a	4.6 a	5.2 a	4.3 a	15.5
2 Year Branch	3.3 a	2.9 a	3.5 a	3.6 a	12.8
3 Year Branch	2.9 a	3.0 a	3.1 a	2.9 a	13.5
4 Year Branch*	2.5	3.3	2.9	2.7	12.1
Current Stem	6.7 a	6.1 a	8.0 a	6.0 a	21.0
1 Year Stem	4.0 a	3.1 a	3.1 a	3.1 a	16.1
2 Year Stem	3.3 a	2.2 b	2.5 b	2.1 a	16.4
3 Year Stem	3.1 a	2.2 b	2.6 ab	2.0 b	18.9
4 Year Stem	2.8 a	2.1 b	2.5 ab	2.0 b	14.6
1 Year Bark	3.9 b	4.2 b	4.5 ab	5.2 a	11.5
2 Year Bark	3.6 ab	3.1 b	4.5 a	4.1 ab	20.2
3 Year Bark	3.6 a	3.7 a	3.9 a	3.6 a	19.4
4 Year Bark*	4.7	3.1	3.9	3.3	26.4
Stump	3.7 ab	3.4 bc	3.8 a	3.1 c	5.8
Roots (>1cm)	2.7 ab	2.6 ab	3.1 a	2.2 b	15.4
Roots (0.25 - 1cm)	2.6 a	2.6 a	3.4 a	2.4 a	19.1
Roots (<0.25cm)	2.8 a	2.3 ab	2.1 ab	1.4 b	21.4

5.4 g) Zinc ($\mu g\ g^{-1}$)

Component	N_0B_0	$N_0B_{7.4}$	$N_{400}B_0$	$N_{400}B_{7.4}$	CV%
Current Needles	30 a	28 a	34 a	26 a	21.3
1 Year Needles	30 ab	32 a	28 ab	23 b	17.4
2 Year Needles	31 a	39 a	35 a	27 a	33.7
3 Year Needles	31 a	51 a	40 a	48 a	34.2
4 Year Needles	58 a	53 a	40 a	56 a	36.5
Current Branch	29 a	25 a	30 a	26 a	11.9
1 Year Branch	29 a	25 a	31 a	24 a	17.3
2 Year Branch	35 a	23 b	27 ab	31 ab	17.1
3 Year Branch	31 a	21 b	26 ab	28 ab	17.1
4 Year Branch	25 a	12 b	26 a	22 a	14.8
Current Stem	20.3 a	17.2 a	21.3 a	17.0 a	20.8
1 Year Stem	13.3 a	9.4 b	11.0 ab	11.1 ab	16.7
2 Year Stem	12.5 a	9.9 a	11.2 a	9.6 a	2.07
3 Year Stem	13.0 a	7.5 b	10.3 ab	9.4 ab	22.0
4 Year Stem	10.4 a	8.1 a	10.1 a	9.3 a	17.8
1 Year Bark	29 a	22 b	25 ab	26 ab	14.1
2 Year Bark	33 a	24 b	33 a	29 ab	15.7
3 Year Bark	39 a	25 b	31 ab	31 ab	14.5
4 Year Bark	36 a	23 b	28 ab	28 ab	19.2
Stump	14.1 ab	12.1 b	16.1 a	13.3 ab	12.9
Roots (>1cm)	9.8 b	10.6 ab	13.8 a	10.0 b	15.7
Roots (0.25 - 1cm)	12.2 a	14.6 a	19.3 a	13.8 a	29.4
Roots (<0.25cm)	12.9 a	13.1 a	16.7 a	12.0 a	30.7

5.4 h) Boron ($\mu g\ g^{-1}$)

Component	N_0B_0	$N_0B_{7.4}$	$N_{400}B_0$	$N_{400}B_{7.4}$	CV%
Current Needles	10.8 b	23.0 a	10.3 b	21.8 a	11.4
1 Year Needles	8.1 c	31.3 a	8.6 c	27.3 b	7.8
2 Year Needles	10.0 c	33.2 a	8.8 c	24.3 b	16.7
3 Year Needles	10.1 c	33.2 a	9.3 c	22.5 b	19.3
4 Year Needles	10.0 c	33.4 a	11.1 c	25.0 b	8.8
Current Branch	12.1 bc	15.3 a	10.5 c	15.0 ab	12.6
1 Year Branch	10.3 b	13.9 a	10.3 b	12.9 a	11.3
2 Year Branch	9.9 b	10.1 b	8.3 b	12.7 a	10.5
3 Year Branch	8.0 a	8.0 a	7.2 a	9.1 a	13.6
4 Year Branch	7.6 a	7.8 a	8.2 a	8.1 a	14.2
Current Stem	12.2 b	17.2 a	11.2 b	15.7 a	10.3
1 Year Stem	3.9 ab	4.7 a	3.7 b	4.7 ab	12.3
2 Year Stem	4.4 ab	5.2 a	3.7 b	4.5 ab	11.0
3 Year Stem	3.6 ab	3.2 b	3.1 b	3.9 a	11.1
4 Year Stem	3.7 ab	3.9 ab	3.5 b	4.2 a	7.2
1 Year Bark	16 c	25 a	14 c	22 b	9.2
2 Year Bark	16 b	24 a	14 b	23 a	10.6
3 Year Bark	18 b	26 a	15 b	23 a	9.6
4 Year Bark	18 b	28 a	15 b	23 a	11.9
Stump	7.4 a	8.7 a	7.9 a	8.5 a	16.5
Roots (>1cm)	9.9 b	13.0 a	9.6 b	13.2 a	8.5
Roots (0.25 - 1cm)	11.6 b	15.9 a	11.8 b	14.9 a	9.1
Roots (<0.25cm)	16.2 b	18.9 a	16.2 b	17.3 ab	8.0

Table 5.5: Effect of N and B fertiliser treatments on root nutrient concentrations of radiata pine trees at Ashley Forest.

Nutrient	Significant fertiliser treatments	Root size affected (cm)	Response
N %	$N_{400}B_{7.4}$	0.25 to 1, <0.25	↑
K %	$N_{400}B_0$, $N_{400}B_{7.4}$	<0.25	↓
Mg %	$N_0B_{7.4}$, $N_{400}B_0$, $N_{400}B_{7.4}$	<0.25	↓
Cu µg g-1	$N_{400}B_{7.4}$	<0.25	↓
Zn µg g-1	$N_{400}B_0$	>1	↓
B µg g-1	$N_0B_{7.4}$, $N_{400}B_{7.4}$	>1, 0.25 to 1, <0.25	↑

5.3.5.1 Nutrient uptake

The actual uptake of nutrients is a product of the size of the tree component and the concentrations of nutrients in them. Fertiliser addition can affect both aspects to varying degrees. Because of the size difference between the fertilised and control trees it would be expected that general nutrient uptake would be greater in the fertilised trees - this depended on the nutrient and the fertiliser treatment (**Appendix 2**).

Both Ca and Mg were present in significantly higher amounts in many of the tree components of the $B_{7.4}$ fertilised trees. The $B_{7.4}$ rate significantly affected the uptake of other nutrients for various ages of the needles and branches and various other components.

The uptake of P, Mg and Zn by the current stem of the $N_{400}B_0$ trees was significantly less than the control. This was most likely due to the much smaller current stem size (see **Figure 5.8**). In general, the uptake of nutrients by the $N_{400}B_0$ trees were significantly higher in 1 to 5 of the 23 components, sampled per nutrient, compared to the control. However when considering the total above-ground uptake of nutrients (**Table 5.6**) only P and K are not significantly greater in the $N_{400}B_0$ trees than the control.

While nutrient uptake was significantly greater in the fertilised trees than the control, some of the nutrient amounts were not in proportion to the increased size of the trees. The total dry weight of the fertilised trees was 190 to 240% greater than the control. Using this as a standard, when considering the proportions of nutrients, one could expect them to be similar assuming that the tree components were also in proportion and general nutrient concentrations had been maintained. Those nutrients that were in excess (>10% higher than expected) were Ca for the $N_{400}B_{7.4}$ treatment and B for the $B_{7.4}$ treatments. The other nutrients were in lower proportions (>10% lower than expected) for at least one of the fertiliser treatments.

Correlations between the presence of the nutrient in the soil and its total tree uptake were not significant. Although the soil samples were taken at the time of the tree biomass, they did not reflect the level of nutrients available for tree uptake over the last 3 to 4 years. Other factors, particularly soil moisture levels during times of rapid growth, may be important parameters controlling nutrient uptake. The differences in the nutrient proportions could be a function of the translocation in supplying nutrients internally for the increased growth of the fertilised trees.

As expected there were significant ($p<.001$) and positive correlations between nutrient uptake and the total above ground dry weight of the trees with the larger trees containing the greatest amount of nutrients.

The stand nutrient contents were in the order: N>K>Ca>P=Mg>Zn>B>Cu which was similar to that found by Madgwick *et al.* (1977) on a good site i.e. N=K>Ca>Mg=P>Zn.

Of the fertiliser added, only a small proportion was taken up by the above-ground parts of the tree one year after fertiliser application. The average N_{400} treated tree had taken up 15.1g of N more than the average control tree. On a hectare basis this would represent an extra 12.6kg in the trees and 3.2% of the N added. The average $B_{7.4}$ tree contained 47.3mg more B than the average control tree which was equivalent to 0.04kg ha^{-1} and represented 0.5% of the B added.

Table 5.6: Average total amount of above-ground nutrients for radiata pine trees in each fertiliser treatment. For each nutrient, means followed by the same letter were not significantly different ($p<.05$).

	N_0B_0	$N_0B_{7.4}$	$N_{400}B_0$	$N_{400}B_{7.4}$
	--- g $tree^{-1}$ ---			
N	14.7 b	26.3 a	27.2 a	32.5 a
P	2.12 b	4.47 a	3.28 ab	3.96 a
K	9.5 b	20.6 a	12.8 b	18.9 a
Ca	3.03 c	7.75 ab	6.28 b	8.35 a
Mg	1.98 b	3.73 a	3.36 a	3.82 a
	--- mg $tree^{-1}$ ---			
Cu	6.9 b	12.9 a	13.2 a	14.3 a
Zn	38.7 b	81.0 a	69.5 a	78.2 a
B	13.3 b	60.3 a	23.2 a	61.0 a

A greater proportion of the added N fertiliser was taken up by the trees compared to the uptake of added B which, even after the luxury consumption and storage of B within the tree, was only a very small proportion of the B added. However, as shown by the B fractionation (**Table 5.3**), much of the added B appeared to be still in the soil and available for further tree uptake. In contrast, the addition of N did not appear to have a long term effect on soil N levels.

5.4 CONCLUSIONS

The addition of fertiliser, particularly B, significantly increased tree growth compared to the control. As a result nutrient uptake was greater in the fertilised trees.

The effect of the fertilisers on nutrient concentrations, where significant compared to the control, was generally positive for the nutrient added by the fertiliser and negative for the other nutrients. The positive effects appeared to be due to the luxury uptake and storage of B and the reduced need to

retranslocate N whereas the negative effects were a result of dilution and retranslocation to meet an increased tree demand for nutrients.

B addition had a large effect on the B concentrations of all components in the treated trees. This result indirectly supports the idea that B may be more mobile within the tree than previously thought. In Chapter 4 the data indicated that B was being redistributed from older to current foliage when B supply is both adequate and limiting.

Retranslocation of nutrients at this site appears to represent an important source of nutrients for new growth. Retranslocation can take place from any of the tree components depending on the nutrient.

The residual affect of the N addition to the site appeared to be short-lived. While 3.2% of the added N was incorporated into the above-ground parts of the tree, there was little evidence of increased N levels in the soil. Losses of N from this site may have included volatilisation, runoff, leaching and uptake by competing vegetation. Runoff may have been significant in moving both the added B and N down slope.

While only 0.5% of the added B was found in the above-ground tree, B appears to have been incorporated into the plant-available soil fractions and will therefore have a longer-term effect in promoting B uptake by the trees.

Various unmeasured factors may have been significant in affecting tree response to the fertilisers including soil moisture levels, the increasing biomass of the competing vegetation, and the size of the tree root system which would govern how much of the soil was exploited for nutrient uptake, the actual amount of nutrient present in the root system and nutrient deficiencies such as P.

Chapter 6

Copper, Zinc and Boron fractions in four New Zealand soil profiles

6.1 INTRODUCTION

Copper, Zn and B deficiencies have been identified in New Zealand radiata pine plantation forestry (Will 1990). Low levels of trace elements in the soil (Turner and Lambert 1991) and trace element imbalances (Birk *et al.* 1991) have also been implicated in growth disorders exhibited by radiata pine on Australian ex-pasture sites. In order to understand the availability of trace elements for plant uptake it is necessary to identify their amounts and distribution within the soil (Shuman 1979).

Total amounts of trace elements in the soil depend on the type of parent material and the degree of weathering (Barber 1984). In New Zealand, Hogg (1988) found total Cu levels in a range of soils to be between 6 and 54μg g^{-1}, while Chowdhury (1990) found total Zn levels in some Canterbury soils to be between 38 and 114μg g^{-1}. Generally total B levels range from 20 to 50μg g^{-1} (Barber 1984). A large proportion of micronutrients in most soils are present in the structure of secondary and primary minerals (J.A. Adams and R.G. McLaren, unpublished).

Trace elements are found in the following soil fractions: soil solution, exchangeable (non-specifically adsorbed), specifically adsorbed by organic and inorganic colloids, organic matter, occluded by soil oxides, and in the primary and secondary minerals (Hogg 1988; J.A. Adams and R.G. McLaren, unpublished). The data so far available from fractionation studies of New Zealand soils have concentrated on the uppermost layers of the soil (i.e the A horizon, Hogg 1988; 0-15cm layer, Chowdhury 1990; A and B horizons, Haynes and Swift 1984).

Sequential fractionation schemes measure the amount of trace element present in each fraction of the soil by sequentially removing that fraction with a selective reagent (Iyengar *et al.* 1981). As fractionation schemes have not been standardised (Shuman 1985) a variety of such schemes can be found in the literature. Examples of single trace element extractions can be found for Cu (e.g. McLaren and Crawford 1973; Hogg 1988), Zn (Iyengar *et al.* 1981, Chowdhury 1990) and B (Jin *et al.* 1987). Multiple trace element fractionation schemes have also been developed such as that described by Shuman (1985) for Mn, Fe, Cu and Zn.

While the concept of the schemes is to divide trace elements in the soil into discrete pools or fractions, as noted by Chowdhury (1990) the extractants used are not entirely specific to individual forms of the trace element.

This chapter describes Cu, Zn and B fractions in four New Zealand soil profiles differing in site, soil type and parent material.

6.2 MATERIALS AND METHODS

6.2.1 Soil sampling

Three soil profiles were sampled by horizon in the Rotorua area. North of Rotorua a complex of Oturoa hill soils (composite yellow-brown pumice from rhyolitic tephra) and Pohatura steepland

soils (steepland soils related to composite soils from rhyolitic tephra on ignimbrite) was sampled under a young agroforest (Taheke agroforest Profile 1) and an adjacent pasture. South of Rotorua a profile of the Haparangi sandy loam (composite yellow-brown pumice soil on yellow-brown loam, Rijkse 1979) was sampled from a mature radiata pine plantation in the Whakarewarewa State Forest.

In Canterbury (Ashley Forest) a profile of the Makerikeri hill soils (yellow grey earth derived from greywacke and loess) under a young radiata pine plantation was sampled at 10cm intervals to a depth of 30cm.

The soil samples were air-dried, ground (2mm) and stored prior to analysis.

6.2.2 Copper and Zinc fractionation scheme

The method used to fractionate Cu and Zn (**Table 6.1**) was developed by Hogg (1988) for Cu and based on the procedures of Shuman (1985) and McLaren and Crawford (1973) as modified by Williams (1981).

Table 6.1: Sequential fractionation scheme for Cu and Zn.

Step	Fraction	Extractant	Soil wt (g)	Conditions
1	Soil solution, exchangeable, organic matter (SEO)	20ml 3% Sodium hypochlorite, NaOCl, pH 8.5	10	Hot water bath, 30 mins. Extraction repeated.
2	Mn oxide	20ml 0.1M Hydroxylamine hydrochloride, $NH_2OH.HCl$, pH 2	2	Shake end-over-end for 30 minutes
3	Amorphous Fe and Al oxides	50ml 0.2M NH_4-oxalate and 0.2M oxalic acid, pH 3	2	Reciprocating shaker for 4 hours in the dark
4	Crystalline Fe and Al oxides	50ml 0.2M NH_4-oxalate, 0.2M oxalic acid & 0.1M ascorbic acid, pH 3	2	Hot water bath for 30 minutes

The same sample of soil was extracted in duplicate throughout the scheme. Plastic centrifuge tubes (100ml) were used and after each extraction step the samples were centrifuged (2000 rpm), filtered (Whatman 42), an aliquot taken for the determination of Cu and Zn levels by atomic absorption spectrophotometry and the remaining soil rinsed with a small portion of distilled water which was then discarded after centrifuging.

Between steps 1 and 2 the soil was air-dried and finely ground with a mortar and pestle.

Throughout the procedure adjustments were made for the loss of soil residue during water rinses and the presence of entrained liquid between extractions.

The total amount of Cu and Zn was measured on the Makerikeri soil samples by a $HClO_4$/HF digestion (see Hogg 1988). The difference between total Cu or Zn and the respective amount extracted during the fractionation scheme was termed the 'residual' fraction.

6.2.3 Boron fractionation scheme

The first two steps of the B fractionation scheme (**Table 6.2**) were based on the methods of Jin *et al.* (1987). Steps 3 and 4 and the general methodology for the B scheme were the same as for Cu and Zn, as described above.

Table 6.2: Sequential fractionation scheme for B.

Step	Fraction	Extractant	Soil wt (g)	Conditions
1	Non-specifically adsorbed	20ml $CaCl_2$	10	Shaken end-over-end 24 hours
2	Specifically adsorbed	20ml 0.01M Mannitol in 0.02M $CaCl_2$	10	"
3	Amorphous Fe and Al oxides	50ml 0.2M NH_4-oxalate & 0.2M oxalic acid, pH 3	2	Shaken end-over-end 4 hours in the dark
4	Crystalline Fe and Al oxides	50ml 0.2M NH_4-oxalate, 0.2M oxalic acid & 0.1M ascorbic acid, pH 3	2	Hot water bath for 30 minutes

Between steps 2 and 3 the soil was rinsed, dried and finely ground with a mortar and pestle.

Boron levels were measured using the azomethine-H method (Wolf 1974, Gaines and Mitchell 1979).

6.3 RESULTS AND DISCUSSION

6.3.1 Copper

Results showed that the majority of fractionated Cu in the Rotorua soils was associated with the amorphous oxide fraction (**Figure 6.1**).

In the upper profile, there was a slight decline in the amount of Cu extracted during the fractionation. However in the Oturoa/Pohatura soil complex under agroforestry the highest amount of Cu extracted was from the horizons at a depth of 70 to 115cm. This increase is mainly due to higher amounts of fractionated Cu being extracted from the amorphous oxide fraction. This same feature was evident from 90 to 110cm in the Oturoa/Pohatura soil complex under pasture and is associated with a buried

soil profile in which previous weathering has released Cu from the parent material. Subsequent volcanic activity buried the soil with new material.

Although both the Rotorua agroforest and pasture profiles are from the same soil series there were large differences in the amount of Cu extracted from the different fractions. In the Oturoa hill soil complex under pasture the amorphous oxide fraction was absent from the second and third horizons with the SEO (soil solution, exchangeable and organic matter) fraction dominant in the second horizon.

In the Makerikeri hill soil Cu was mainly associated with both the SEO and crystalline oxide fractions. Below 10cm the Mn and amorphous oxide fractions became more evident. Levels of Cu extracted from this soil during the fractionation were low, averaging 1.5μg g^{-1}, compared to the Rotorua soils which ranged from 2 to 8.5μg g^{-1} in the top 30cm of the profile.

The total amount of Cu found in the Makerikeri profile was 4.2, 4.2 and 3.7μg g^{-1} in the 0 to 10cm, 10 to 20cm and 20 to 30cm depths respectively. The amount of Cu extracted during the fractionation scheme represented less than half the total Cu (**Figure 6.2**). Thus the major fraction was residual, particularly at the 10 to 20cm depth.

These Cu totals are below the range of 6 to 54μg g^{-1} of total Cu described by Hogg (1988).

6.3.2 Zinc

In the Rotorua soils, the fractionated Zn was more evenly distributed between the fractions (**Figure 6.3**) than the Cu fractions. Greatest concentrations were found in the Mn and amorphous oxide fractions, with the SEO Zn representing an important fraction in the Ah horizon. Down the profile the fractionated Zn levels fluctuated with an increase occurring in the same horizons as Cu in the Oturoa/Pohatura soil complex under agroforestry and pasture. This increase was associated with all of the oxide fractions rather than being associated with only the amorphous oxides as was the case for fractionated Cu.

In the Haparangi sandy loam Zn levels declined sharply down the profile becoming increasingly associated with the crystalline oxide fraction. However at the base of the profile the levels of Zn increased as the Mn and amorphous oxide fractions of Zn reappeared. This change was not noted for Cu.

There was a slight increase in the levels of Zn fractions down the profile of the Makerikeri hill soil at Ashley Forest. Zn was predominantly in the crystalline oxide fraction. As with Cu, the overall amount of Zn extracted (about 10μg g^{-1}) was generally less than the 4 to 30μg g^{-1} from the top 30cm of the Rotorua soil profiles.

During the fractionation procedure there was a large variation in the amount of Zn extracted from the Mn and amorphous oxide fractions in the duplicate samples. This problem has been found before when using this particular fractionation scheme for Zn (L. Hassall, pers. comm., 1992). Chowdhury (1990) did not have problems with the oxide replicates for Zn but noted poor replication for the organically bound fraction. Shuman (1985) found this method to be satisfactory.

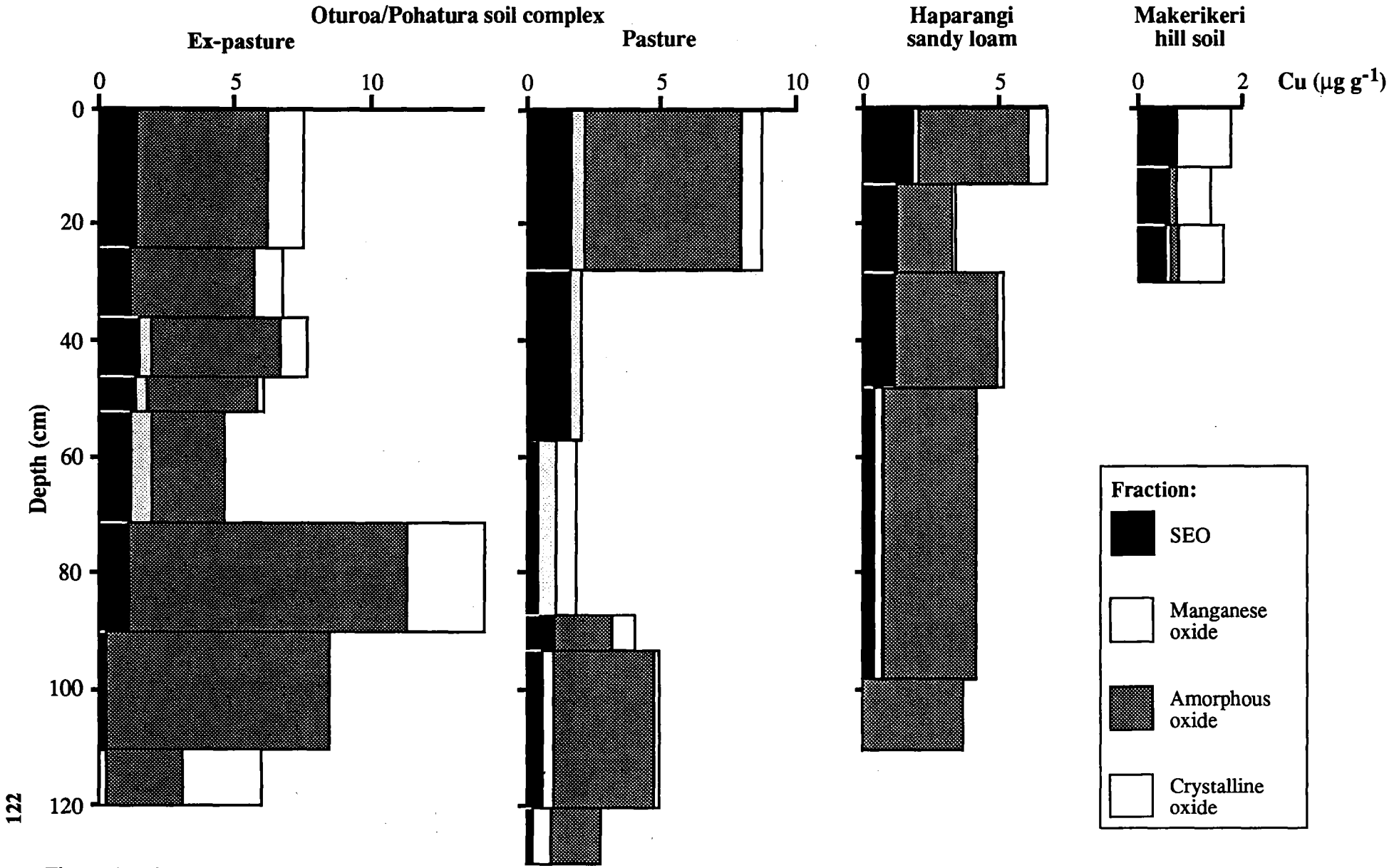


Figure 6.1: Copper fractions in four New Zealand soil profiles.

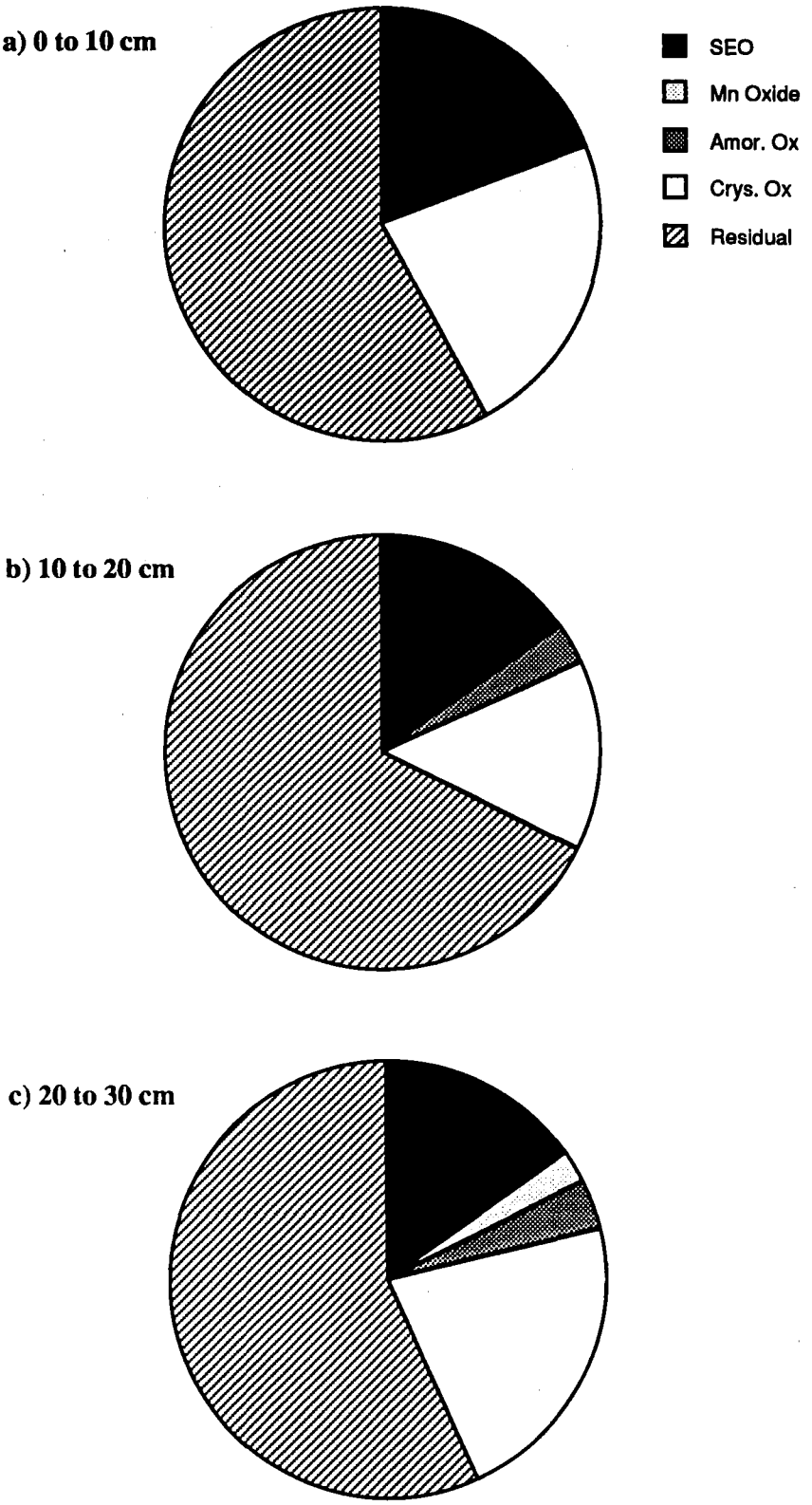


Figure 6.2: Copper fractions, as a proportion of the total copper, in three depths of the Makerikeri hill soils at Ashley Forest.

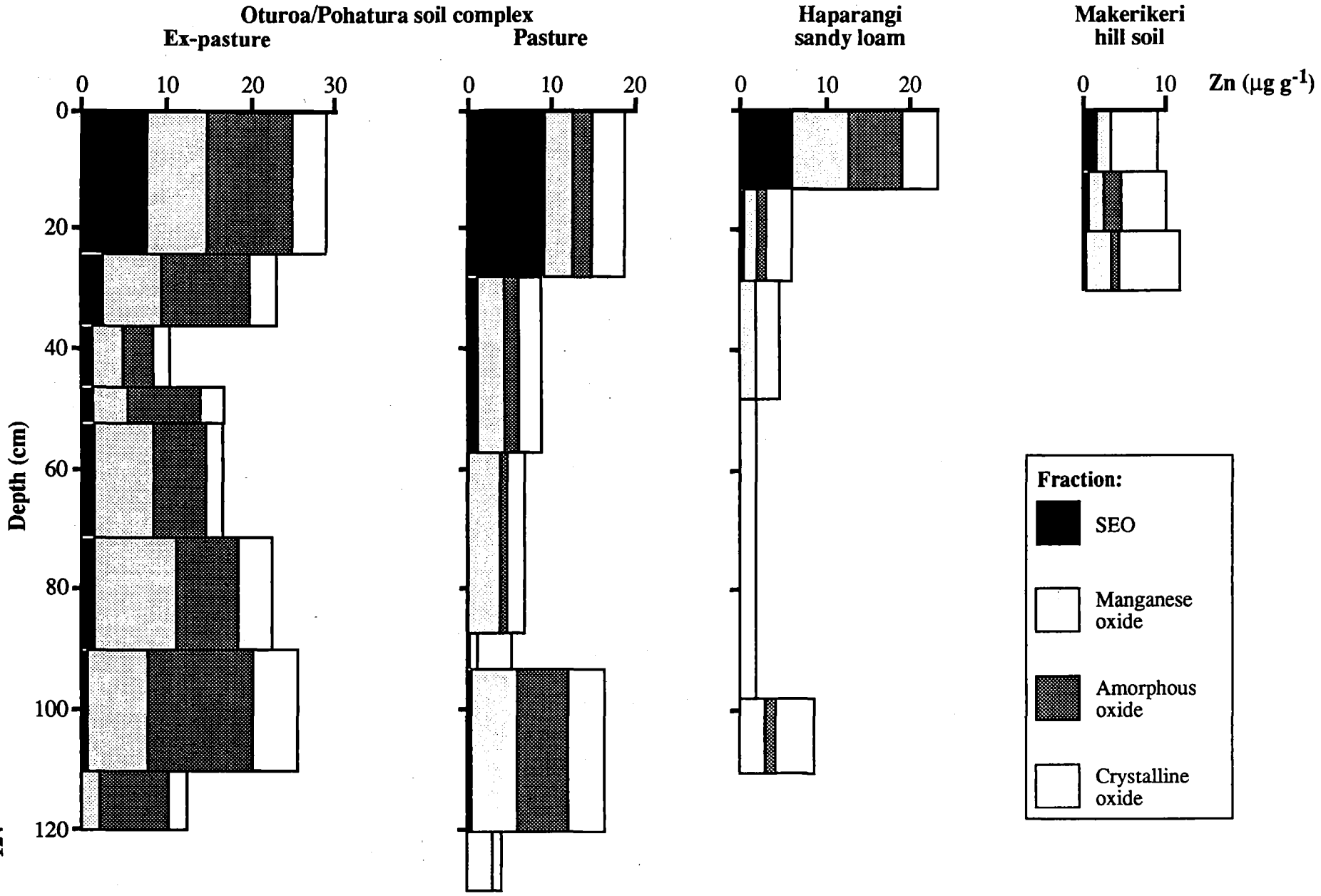


Figure 6.3: Zinc fractions in four New Zealand soil profiles.

The total amount of Zn in the 0 to 10cm, 10 to 20cm and 20 to 30cm depths in the Makerikeri profile was 24, 22 and 23μg g^{-1} respectively. As with Cu, these Zn totals are below the 38 to 144μg g^{-1} range found by Chowdhury (1990) for some Canterbury soils.

While total Zn did not vary with depth in the Makerikeri profile, the proportion of total Zn extracted in the fractionation scheme increased from 37% at 0 to 10cm to 49% at a depth of 20 to 30cm **(Figure 6.4)**.

6.3.3 Boron

B was almost entirely associated with the amorphous and crystalline oxide fractions in all three soils **(Figure 6.5)**. The fractionation extracted between 4 and 11μg g^{-1} of B with levels generally declining down the profile.

In the Oturoa/Pohatura soil complex the amount of B extracted in the fractionation scheme increased at depth - as was noted for Cu and Zn. At the base of the agroforest profile the non-specifically and specifically adsorbed fractions reappeared as did the amorphous oxide fraction. This did not occur in the pasture profile where the amorphous oxide fraction dominated the horizons below 28cm depth.

Unlike Cu and Zn, the amount of B fractionated from the Makerikeri profile was similar to the amount extracted from the upper horizons of the Rotorua profiles.

6.3.4 General

Both the Cu and Zn data from the Oturoa/Pohatura soil complex, under agroforestry and pasture, indicated the presence of a buried soil. In the agroforestry profile the horizons of the buried soil were found at a depth of 70cm while in the pasture profile this occurred at approximately 90cm. These horizons probably represent the same buried soil which has been subject to different erosional and depositional histories at the two sites.

The B data confirm the presence of a buried soil in the Oturoa hill soil complex under pasture but not under the agroforest profile.

In the Haparangi sandy loam profile the Zn data also suggests the presence of a buried soil but this was not confirmed by the Cu or B results.

The fractionation schemes used did not extract the residual trace element fraction which is the amount of the trace element in resistant forms associated with sand, silt, clay and organic fractions in the soil (Hogg 1988). The proportion of the trace element represented by the residual fraction depends on the degree of soil weathering.

In the Makerikeri profile the residual fraction was dominant representing 57 to 68% of total Cu and 51 to 63% of total Zn.

It should be noted that attempts were made to measure total B in the Makerikeri profile by the fusion method but difficulties were encountered when determining the resulting B colorimetrically.

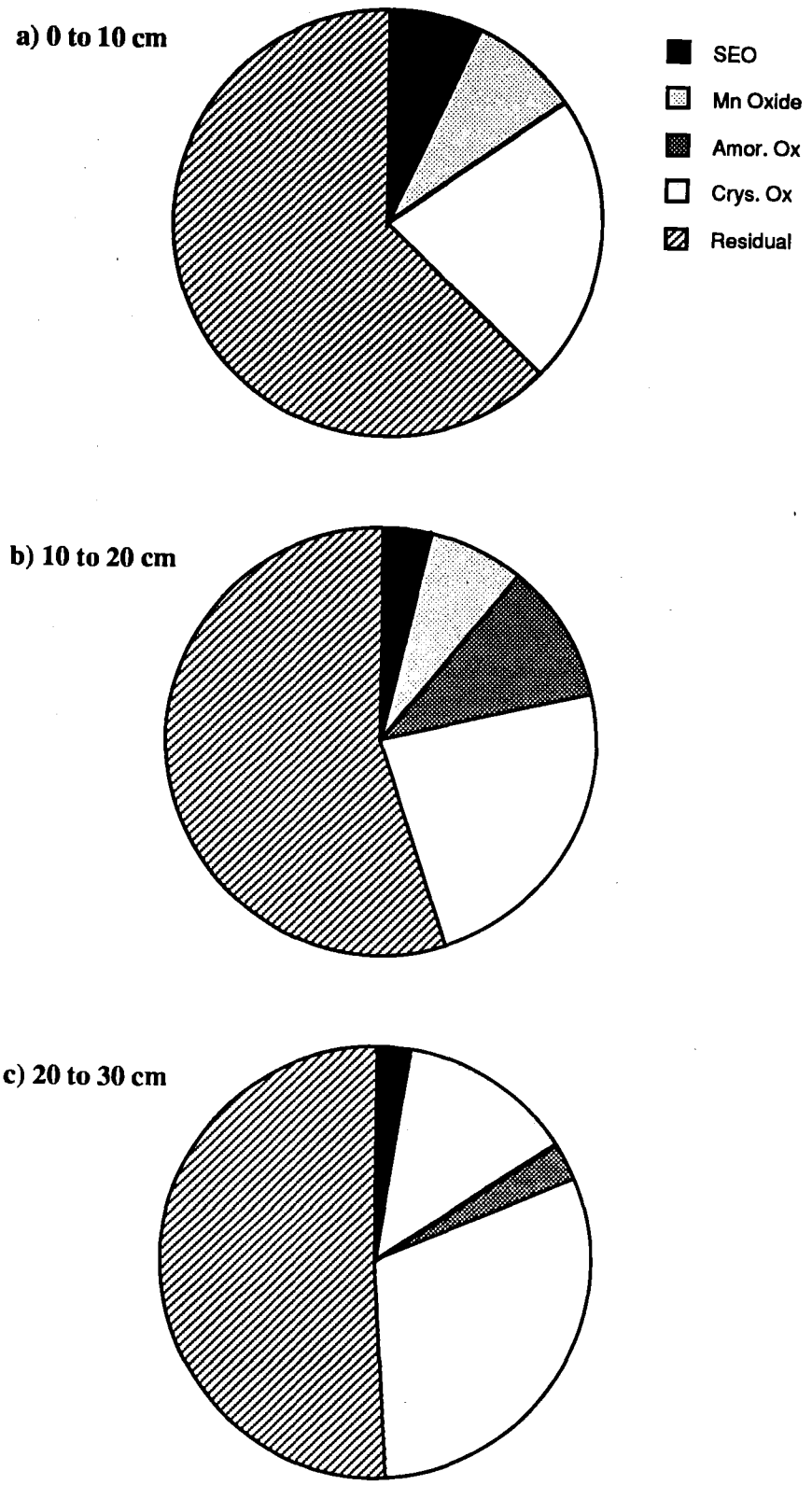


Figure 6.4: Zinc fractions, as a proportion of the total zinc, in three depths of the Makerikeri hill soils at Ashley Forest.

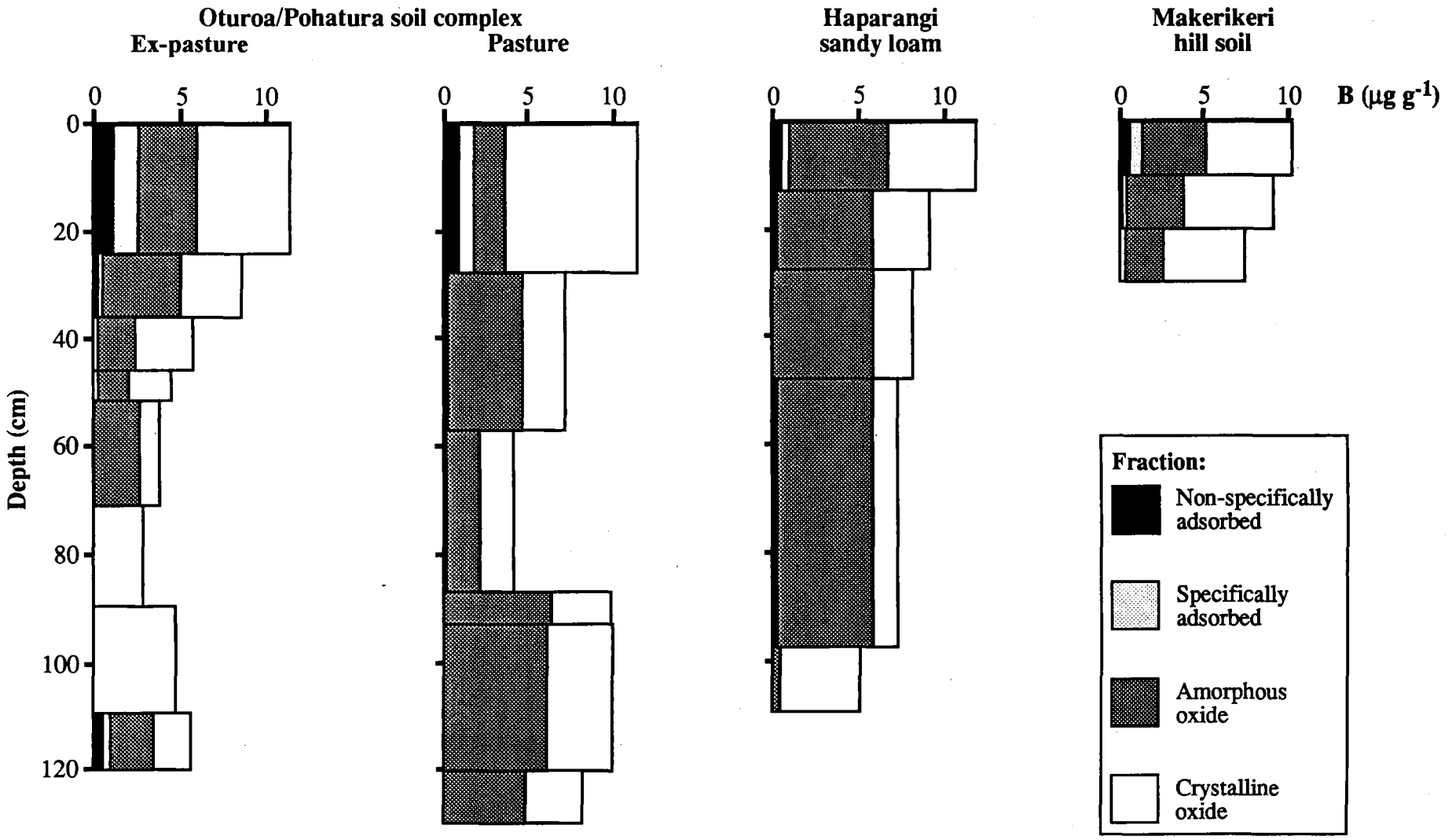


Figure 6.5: Boron fractions in four New Zealand soil profiles.

The total amounts of Cu and Zn extracted from the Makerikeri soil appear to be extremely low when compared to the recent data of Hogg (1988) and Chowdhury (1990). The Makerikeri profile results for total Cu and Zn further highlight the low nutritional status of this forest soil. However, it should be noted that, to date, neither of these two micronutrients have been identified as being deficient for radiata pine growth at Ashley Forest.

6.4 CONCLUSIONS

Fractionation schemes do differentiate trace elements into 'fractions' but variations in the method can occur particularly for Zn.

At Rotorua the total amounts and the distribution of Cu, Zn and B between the fractions varied down the profile and was related to the soils complex morphology, as a result of periodic volcanic deposition and erosional processes, and the subsequent burial of soils at depth. For the Canterbury soil, there was less variation in the total amounts and distribution of the trace elements down the profile.

Chapter 7

The effect of N source on growth and macro- and micro-nutrient uptake of Pinus radiata seedlings in a sand culture experiment.

7.1 INTRODUCTION

Generally it is considered that pines utilise ammonium nitrogen (NH_4^+-N), rather than nitrate N (NO_3^--N) as a nitrogen source, and grow in soils where the conditions are not favourable for nitrification (Haynes and Goh 1978). Various pine and fir species have shown better growth, during non-sterile soil-less pot trial investigations, with ammonium, rather than nitrate, as the source of N, e.g Pinus contorta (Bigg and Daniel 1978), Pseudotsuga menziesii (Van den Driessche 1971, Van den Driessche and Dangerfield 1975), and Pinus radiata (McFee and Stone 1968). However, radiata pine (Pinus radiata) is increasingly grown on old pasture soils where there is a high rate of NO_3^--N production (Carlyle *et al* 1989) and presumably nitrate could be a major source of available inorganic N in these situations.

The source of N, either as ammonium or nitrate, influences the uptake of other plant nutrients. It appears that NH_4^+, Ca^{2+}, Mg^{2+}, and K^+ compete with each other during their accumulation by plants (Haynes and Goh 1978). Ammonium-N nutrition generally enhances the uptake of phosphate and sulphate (Blair *et al* 1970) while at a given pH, the uptake of Ca, Mg and K is usually higher for nitrate-grown plants than those grown with ammonium (Pilbeam and Kirkby 1992). Studies on nutrition and fertilisers indicate that there can be an imbalance between N (as nitrate) and other essential elements absorbed as anions such as sulphur and phosphate (Birk *et al* 1991). When nitrate is the N source the uptake of sulphur and phosphorus appears to be reduced.

Another important aspect of the source of N is its effect on rhizosphere pH. According to Nye (1981) plant absorption of nitrate tends to raise the rhizosphere pH while absorbing ammonium lowers pH. Such changes will affect a number of rhizosphere characteristics including the concentrations of both macro- and micronutrients.

Much recent pot trial work with pines and nitrate-N nutrition appears to be centred on nitrate reductase activity (NRA) and the ability of the seedlings to function under high nitrate levels (e.g. Adams and Attiwill 1982). Many interrelationships exist among the factors regulating NRA making it a complex area not yet fully understood (Haynes 1986a).

A variety of pot trial methods, involving non-soil media and a range of nutrient additions, have been used to investigate the growth and nutrition of tree species. The examples in **Table 7.1** suggest that there is a range of nutrient concentrations within which 'normal' plant growth will occur. For N addition, radiata pine has been grown satisfactorily at rates of N addition ranging from 2μg N ml^{-1} (McFee and Stone 1968) up to 105μg N ml^{-1} (Will 1961).

For non-soil pot trials there are a number of important considerations including the choice of media, the rate of addition and maintenance of nutrient concentrations, the prevention of salt build up, the age and number of the seedlings and the duration of the trial. The media should be stable, inert, free of contaminants and have adequate water holding and aeration characteristics. The most common non-soil medium used appears to be sand (see **Table 7.1**).

Table 7.1: The concentrations of nutrients (mg ml^{-1}), pH levels, and type of culture that have been used to grow radiata pine seedlings in previous pot trial experiments.

a) Macronutrients

Author and culture	Species	pH	N	P	K	Ca	Mg	S
Will (1961) - water	Radiata pine		105*	1	5-10	-	10	
McFee and Stone (1968) - soil, soln., resin	Radiata pine	3.6 5.9	22.4*					
Van den Driessche (1971) - sand, soil	Douglas fir, spruce, w. hemlock	5.4 7.5	50@	30	200	150	50	123-180
Van den Driessche and Dangerfield (1975) - sand	Douglas fir	6.9	50*	10*	200	150	50	66-237
Bigg and Daniel (1978) - sand, perlite	Lodgepole pine, Douglas fir, spruce		21	6.2	23.4	50	4.9	13-37
Adams and Attiwill (1982) - sand#	Radiata pine	5.6	42@	8	27.3	60	56	74-122

* Was found to be the optimum level during experimentation.

@ Varying proportions of ammonium-N and nitrate-N.

The nutrient concentrations used were adapted from Bigg and Daniel (1978).

b) Micronutrients.

	Cu	Zn	B	Fe	Mn	Mo+
Van den Driessche (1971)	0.02	0.02	0.2	6	0.2	0.003
Bigg and Daniel (1978)	0.005	0.0125	0.125	2	0.125	0.0025
Adams and Attiwill (1982)	0.005	0.01	0.1	-	-	-

+ Mo = molybdenum

Once nutrient solutions have been added, nutrient loss from the rooting medium via leaching and volatilisation may also be an important for N from ammonium addition mainly due to the high glasshouse temperatures which, according to McLaren and Cameron (1990), can enhance the gaseous loss of N.

The nutrients in the solution can be maintained at constant concentrations by several methods including sub-irrigating the pots (Van den Driessche 1971, Van den Driessche and Dangerfield 1975) or by the regular addition of fresh nutrient solution to the media surface by hand or automated drip feed (Bigg and Daniel 1978, Adams and Attiwill 1982). In both cases, the pots require frequent flushing with water to prevent salt build up.

The age of seedlings at the start of pot trials can vary and are commonly three weeks old (e.g. Van den Driessche and Dangerfield 1975) to 3 months old (e.g. McFee and Stone 1968) with weak nutrient solutions being added to maintain the seedlings prior to the actual experiment beginning (Adams and Attiwill 1982). Trials in non-soil culture tend to be short and can range from 3 weeks (McFee and Stone 1968) to 4 months (Van den Driessche 1971). Factors which may affect trial duration include the health of the seedlings, the time to produce treatment effects and the production of sufficient biomass for analysis.

Generally a number of seedlings are transplanted into each pot. This reduces the variability due to non-uniform seedling growth and genetic diversity (Allen *et al* 1976).

To date non-soil pot trials with radiata pine have focussed on the effect of N source on growth, macronutrient uptake, and, more recently, nitrate reductase activity. The research described here investigated the effect of the source and rate of N on the macronutrient and micronutrient uptake of radiata pine seedlings growing in sand culture under semi-controlled (glasshouse) conditions.

7.2 MATERIALS AND METHODS

7.2.1 Sand culture pot trial

Radiata pine seed (GF 17) was soaked for 2 days in distilled water and then germinated in washed river sand[1]. In mid-February, 1991, the 2 week-old seedlings were planted out into pots of the washed river sand (volume of 2.6*l*), at the rate of 5 seedlings pot^{-1}, in a glasshouse where the temperature ranged from 15 to 25°C. A fibre-glass mesh was used to prevent sand loss through pot drainage holes. The pots were placed on wooden slatted tables to allow for free drainage.

The seedlings were maintained for 6 weeks using a nutrient solution containing NO_3^--N or NH_4^+-N at 7μg ml^{-1}, P at 1μg ml^{-1}, K at 21μg ml^{-1}, Ca and Mg at 5μg ml^{-1} and S at 7μg ml^{-1}. This solution was added twice a week after the previous nutrient solution had been flushed from the pots with 1.2*l*[2] of deionised water.

At 2 months of age the seedlings received one of 6 treatments (**Table 7.2**), in a volume of 600ml of deionised water[3], which was added twice a week after flushing out the old solution. Six replicates allowed for 2 harvest dates, 3 pots at 2 months (harvest 1) and a further 3 pots at 4 months (harvest 2) from the beginning of nutrient treatment solution addition. The nutrient solutions were based on those used by Adams and Attiwill (1982) and M. Andrews (pers. comm. 1990). The pH of the added solutions ranged from 6.2 to 6.4.

Varying rates of K_2SO_4 were added in the treatment solutions to provide a constant K concentration of 195μg ml^{-1} which was the maximum amount of K supplied in the nitrate-N_{70} treatment (i.e treatment 6 in **Table 7.2**).

The replicate pots from each treatment were placed in blocks along the tables to distribute the treatments as evenly as possible in the glasshouse area as the pots were not moved during the experiment.

At harvesting the shoots and roots were separated. The roots were washed in deionised water and the excess water removed with paper towels. The shoots and roots were weighed and the shoot heights measured. At harvest 2, two measurements were taken to describe seedling height - 'pot'

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[1] The sample of the sand was tested for the presence of carbonates using dilute HCl. The results indicated that carbonates were absent. The sand was then washed in water to remove most of the finest sand fractions (<0.25mm) and dried.

[2] This amount of water was greater than the total pore volume of 1.1*l*, in each pot, to ensure that the old nutrient solution was fully flushed out before the new solution was applied.

[3] It was considered that a volume of 600ml would provide nutrients in the rooting zone while minimising the amount of nutrients lost from the pot by drainage.

height and 'actual' height (**Figure 7.1**). Pot height was the height of the seedlings as they were growing in the pot just prior to harvesting. When the seedlings were stretched out, after harvesting, to remove the deviations, the actual seedling height could be measured. The difference between these two height measurements was termed the 'height difference'.

Table 7.2: The nutrient concentrations present in each treatment of the N source and rate sand-culture pot trial with radiata pine seedlings.

a) Macronutrients

Nutrient	Rate $\mu g\ ml^{-1}$	Treatment Number	Compound	Other nutrients added ($\mu g\ ml^{-1}$)
NH_4^+-N	14	1	$(NH_4)_2SO_4$	S = 16.0
	35	2		40.1
	70	3		80.2
NO_3^--N	14	4	KNO_3	K = 39.1
	35	5		97.8
	70	6		195.5
P	8	All	KH_2PO_4	K = 10.1
K	97.7	5	K_2SO_4	S = 40.1
	156.4	4		64.1
	195.5	1,2,3		80.1
Ca	60	All	$CaCl_2.6H_2O$	Cl = 106.2
Mg	50	All	$MgSO_4.7H_2O$	S = 66

b) Micronutrients

Cu	0.01	All	$CuCl_2.2H_2O$	Cl = 0.011
Zn	0.01	"	$ZnCl_2$	Cl = 0.011
B	0.1	"	$Na_2B_4O_7.10H_2O$	Na* = 0.106
Mn	0.125	"	$MnCl_2.4H_2O$	Cl = 0.161
Mo	0.003	"	$Na_2MoO_4.2H_2O$	Na = 0.0014
Co*	0.1	"	$CoSO_4.7H_2O$	S = 0.054
Fe	2	"	EDTAFeNa	Na = 0.82

* Na = sodium, Co = cobalt.

The replicate shoot and root samples were then dried (60°C), weighed, and ground (<1mm). The root samples from harvest 1 were bulked per treatment in order to provide sufficient sample for subsequent chemical analysis.

Macronutrient levels of N, P, K, Ca, and Mg were determined following a H_2SO_4/H_2O_2 digestion. N and P levels were measured on an auto-analyser and K, Ca, and Mg on an atomic absorption spectrophotometer (Shimadzu) as described by Nicholson (1984).

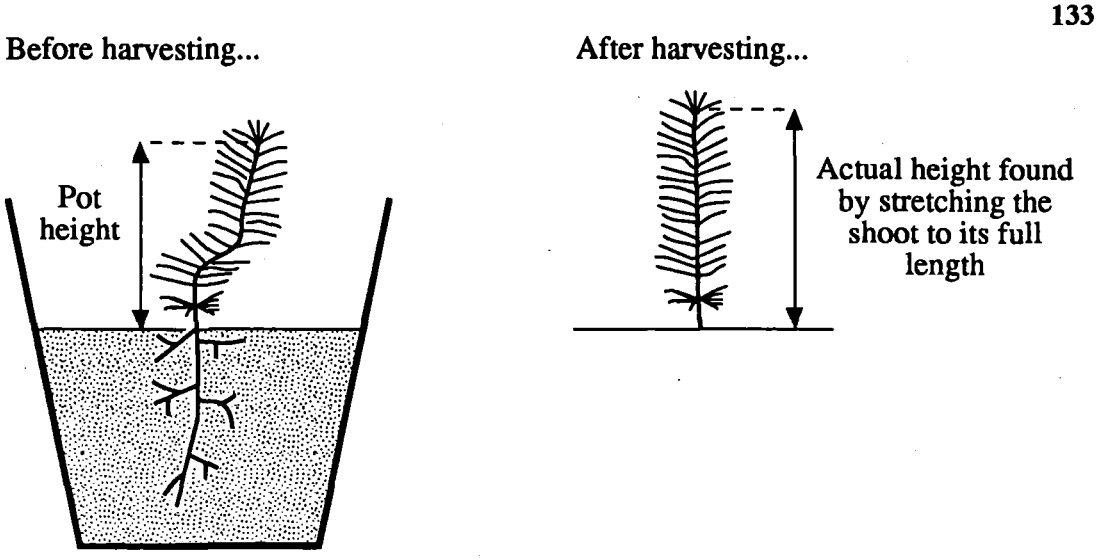

Figure 7.1: Measurement of radiata pine seedling 'pot' height and actual seedling height at harvest 2 of the sand culture pot trial.

The levels of micronutrients were found using a dry-ashing technique at 600°C for 1 hour with the ash being extracted in 10ml of 0.5M H_2SO_4. The filtered (Whatman 40) solution was analysed for Cu, Zn and Fe contents by atomic absorption spectrophotometry and for B using the azomethine-H technique (Wolf 1974, Gaines and Mitchell 1979).

7.2.2 Calculations

From the harvest 2 data, the following parameters were calculated:
a) shoot:root ratios,

$$\frac{\textit{Dry weight of shoots (g pot}^{-1}\textit{)}}{\textit{Dry weight of roots(g pot}^{-1}\textit{)}}$$

b) total nutrient content of the seedlings per pot,

$$\textit{Amount of nutrient in the shoot (g pot}^{-1}\textit{) + amount of nutrient in the root (g pot}^{-1}\textit{)}$$

and c) the proportion (%) of total seedling micronutrient found in the seedling shoots:

$$\frac{\textit{Amount of micronutrient in the shoot (}\mu\textit{g pot}^{-1}\textit{)}}{\textit{Total amount of micronutrient in the seedling (}\mu\textit{g pot}^{-1}\textit{)}} \times 100$$

7.2.3 Statistics

Data were subjected to analysis of variance (ANOVA) using the computer program GENSTAT. For each harvest (unless otherwise stated) the following effects were examined separately:

(i) The effect of the increasing rates of N source (ammonium or nitrate) addition, and interactions, on seedling shoot and root dry weights, shoot:root ratios, actual seedling height, and the seedling height difference (harvest 2 only).
(ii) The effect of the increasing rates of N source (ammonium or nitrate) addition, and interactions, on nutrient concentrations in the shoots and roots, total nutrient uptake by the seedlings (harvest 2 only) and the partitioning of micronutrients between the seedling shoots and roots (harvest 2 only).

The Least Significant Difference (LSD) test was used to compare mean values.

Detailed results are presented in Appendix 3.

7.3 RESULTS

7.3.1 Physical parameters

7.3.1.1 Seedling weights

At harvest 1 the shoot dry weights were not significantly affected by the source of N, ammonium or nitrate, or the rate of N addition. Average shoot weights were 4.4g pot^{-1} for the ammonium-fed seedlings and 4.0g pot^{-1} for the nitrate-fed seedlings. In contrast the root dry weights had been significantly affected by the N source. The roots of the ammonium-fed seedlings were significantly ($p<.05$) heavier at an average of 0.48g pot^{-1} compared to 0.40g pot^{-1} for the nitrate-fed seedlings. The rate of N had no effect on root dry weights.

At harvest 2, the shoot dry weights were significantly affected by the source ($p<.001$) and rate ($p=.002$) of N (**Figure 7.2**). The average shoot dry weight for the ammonium-fed seedlings was 7.9g pot^{-1} compared to 5.9g pot^{-1} for the nitrate-fed seedlings. With an increase in ammonium-N addition from 14 to 35μg g^{-1} the shoot weight significantly increased (**Figure 7.2**). The form of N had a significant ($p=.002$) effect on root dry weight with an average of 2.3g pot^{-1} produced by the ammonium-fed seedlings compared to 1.7g pot^{-1} for the nitrate-fed seedlings.

7.3.1.2 Shoot heights

At harvest 1 the source of N had had a significant effect ($p=.025$) on seedling height with the ammonium-fed seedlings having an average height of 14.9 cm and the nitrate-fed seedlings 14.0 cm.

At harvest 2 the effect of N-source was more significant ($p<.001$) and the rate of N addition was also significant ($p=.016$). The ammonium-fed seedlings were significantly taller (**Figure 7.3**) than the nitrate-fed seedlings where N was added ta a rate of 70μg ml^{-1}. The height of the ammonium-fed seedlings significantly increased as the rate of N increased from 14 to 70μg ml^{-1}. The nitrate-fed seedlings had a significant height increase as N addition increased from N_{14} to N_{35}.

The tallest seedlings, at an average of 29cm, were produced by the 70μg NH_4^+-N ml^{-1} treatment and the shortest, at 25cm, by the 14μg NO_3^--N ml^{-1} treatment.

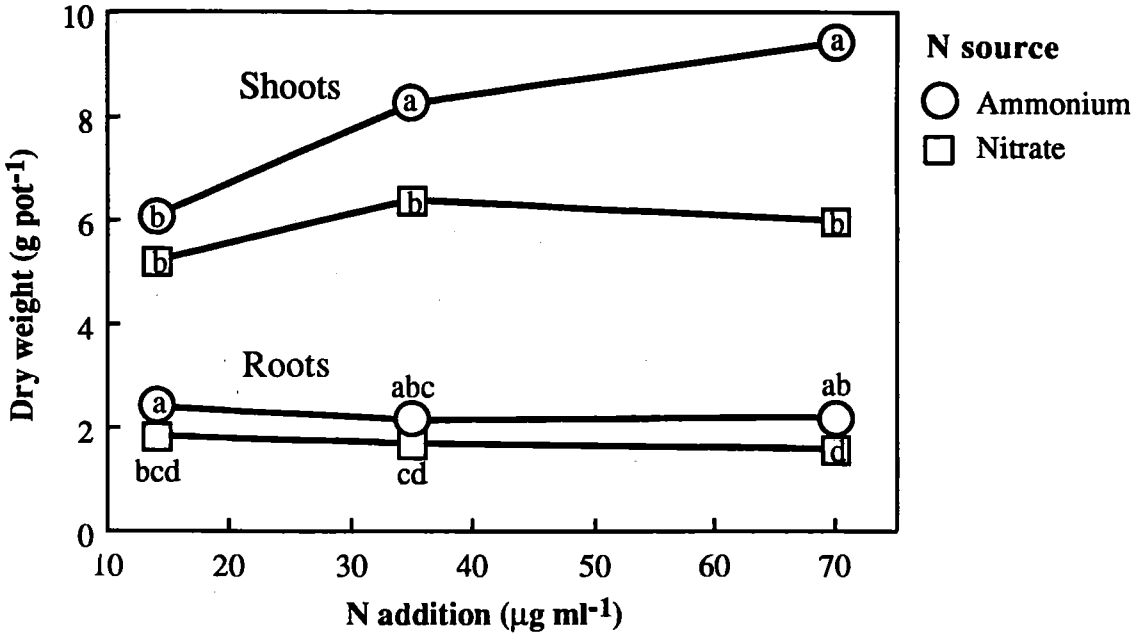

Figure 7.2: Effect of N source and rate on the dry weight of radiata seedling shoots and roots at harvest 2. For shoots or roots, mean values with the same letter were not significantly different ($p<.05$).

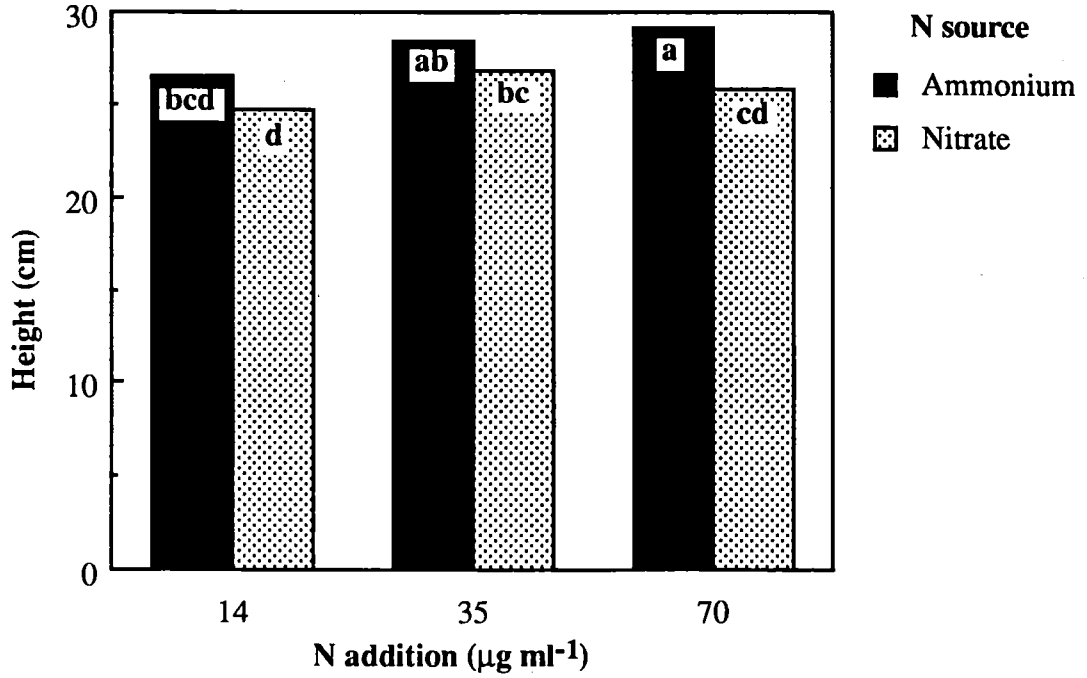

Figure 7.3: Effect of N source and rate on the actual seedling height at harvest 2. Means with the same letter were not significantly different ($p<.05$).

7.3.1.3 Seedling height difference

The raw data for this measurement were skewed - the range was 0.0 to 8.3cm with a mean of 1.6cm. A squareroot transformation of the raw data indicated that the squareroot of the height difference had been significantly affected by the source of N ($p=.028$) and particularly the rate of addition ($p=.003$). The height differences were greatest for the ammonium-fed seedlings but this was only significant ($p<.05$) at the N_{14} rate (**Table 7.3**).

With an increase in nitrate-N addition from 14 to 35μg ml^{-1}, the height difference increased from 0.4m to 1.7cm. At the N_{35} and N_{70} rates of N addition there was no significant difference between the N sources.

7.3.1.4 Shoot to root ratio

At harvest 2 the shoot dry weight to root dry weight ratio was significantly affected ($p<.001$) by the rate of N addition rather than by the source (**Figure 7.4**). The addition of N at 35 and 70μg ml^{-1} resulted in shoot to root ratios significantly higher, at an average of 3.8 and 4.1 respectively, than the 2.7 of the N_{14} treatment.

Table 7.3: Effect of N source and rate on the height difference of the shoots of radiata pine seedlings at harvest 2. For each nutrient, means with the same letter (in brackets) were not significantly different ($p<.05$). Least significant differences were calculated on a squareroot transformation of the raw data.

N source	N rate (μg ml^{-1}) 14	35	70
		--- cm ---	
Ammonium	1.4 (a)	2.2 (a)	2.0 (a)
Nitrate	0.4 (b)	1.7 (a)	1.6 (a)

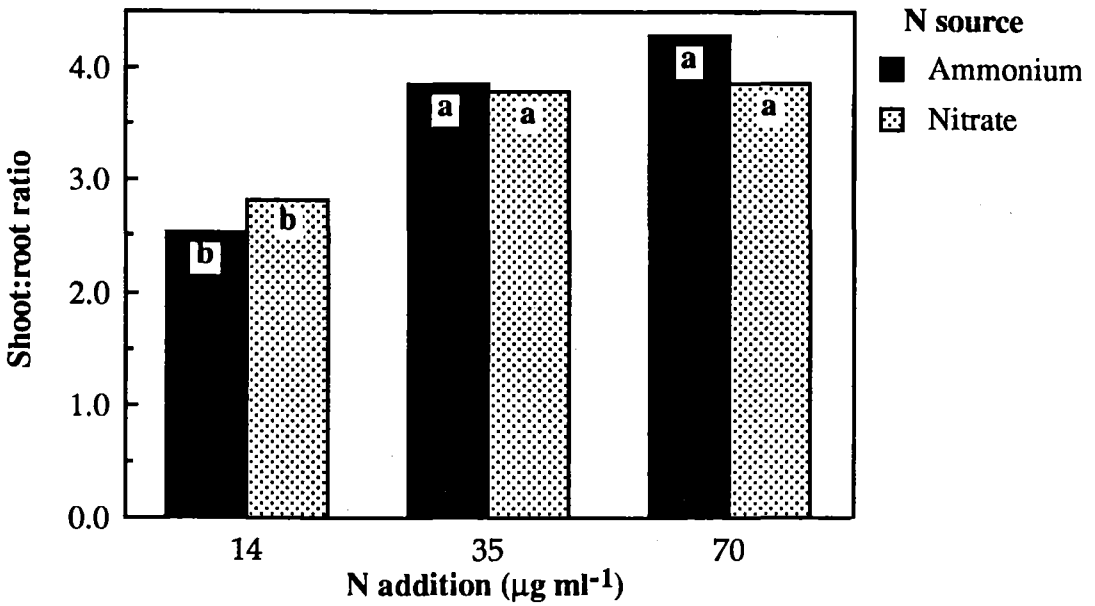

Figure 7.4: Effect of N source and rate on the shoot:root ratio of radiata pine seedlings at harvest 2 of the sand culture pot trial.

7.3.2 Nutrient parameters

7.3.2.1 Nutrient concentrations

At harvest 1, the source of N significantly ($p<.001$) affected the concentrations of N, P, Ca, Mg, B and Fe in the shoots with ammonium and nitrate increasing the concentrations of different nutrients (**Table 7.4a**). When ammonium was the source of N, those nutrients with significantly higher concentrations than the nitrate-fed seedlings were N, P, B and Fe. When nitrate was the N source

the concentrations of Ca and Mg were significantly higher. For the other nutrients (K, Cu and Zn) there was no significant difference between the two sources of N.

The rate of N only significantly (p=.012) affected the shoot concentration of N which increased with increasing N rate.

In the roots at harvest 1, the source of N significantly affected the concentrations of Ca (p=.029), Mg (p=.015), B (p=.008) and Fe (p=.015). In all cases the concentrations of these nutrients were greater in the roots of the nitrate-fed seedlings.

At harvest 2 the source of N significantly (p<.001) affected the shoot concentrations of P, Ca, Mg, Cu and Fe and also for B (p=.010). The concentrations of P, Cu, B and Fe were significantly higher (p<.05) for the ammonium-fed shoots (**Table 7.4b**) while Ca and Mg were significantly higher (p<.05) in the nitrate-fed shoots. The rate of N addition significantly affected N (p<.001) and Fe (p=.007) where both shoot N and Fe concentrations increased with increasing N rate.

At harvest 2, significant N source by rate interactions were measured for the shoot concentrations of N (p=.040), K (p=.013), Ca (p=.003) and Mg (p=.088). The concentration of N in the nitrate-fed shoots increased steadily from 1.6, at N_{14}, to 2.1% at N_{70} but in the ammonium-fed shoots increased from 1.6 at N_{14} (i.e. 14μg N ml^{-1}) to 2.1% for both the N_{35} and N_{70} treatments. The shoot concentrations of K, Ca and Mg decreased with increasing rates of NH_4^+-N and increased with increasing NO_3^--N rates.

Nutrient concentrations in the roots from harvest 2 were all (except Zn) significantly (p<.05) affected by N source. The concentrations of N and P were higher in the roots of the ammonium-fed seedlings while K, Ca, Mg, B and Fe were higher in the nitrate-fed roots.

The rate of N addition had significant effects on the root concentrations of N and P (p<.001), K (p=.003), Mg (p=.011) and Fe (p=.034). With increasing rates of N, N% increased - particularly for the ammonium-fed roots - while P, K and Fe concentrations decreased. For Mg and Ca the effect of the rate of N depended on its source.

The concentration of Ca in the ammonium-fed roots decreased and were half that in the nitrate-fed roots where Ca% increased with increasing N rate (**Figure 7.5a**). The Mg concentrations in the ammonium-fed roots were fairly constant with increasing N rate and about a third of the Mg% in the nitrate-fed roots where Mg% increased with N rate (**Figure 7.5b**).

This interaction between N source and rate significantly affected Ca (p<.001) and Mg (p=.004) and also for Cu (p=.018). The concentrations of Cu were not significantly different with increasing rates of NH_4^+-N addition but with NO_3^--N, Cu doubled from 9μg g^{-1}, at N_{14}, to 18μg g^{-1} at N_{70}.

At harvest 2 the concentrations of Cu, B and Fe were significantly higher in the roots of the nitrate-fed seedlings but significantly lower in the shoots compared to the ammonium-fed seedlings (**Table 7.4b**). This was also measured for B and Fe at harvest 1 (**Table 7.4a**).

Between harvests 1 and 2 there were significant (p<.01) changes in all of the shoot nutrient concentrations, for each N source, which all (except Mg) decreased (**Table 7.4**). In the roots there were significant (p<.05) differences for N, Ca, Cu and B. Between the two harvests the root concentrations of N, Cu and Zn decreased while P, Ca and Mg increased.

Table 7.4: Effect of N source on the nutrient concentrations of the shoots and roots of radiata pine seedlings grown in sand culture at harvest 1 and harvest 2. For each nutrient, means with the same letter were not significantly different ($p<.05$).

a) Harvest 1

	N	P	K	Ca	Mg	Cu	Zn	B	Fe
	--- % ---					--- µg g^{-1} ---			
Shoots:									
Ammonium	3.04 a	0.489 a	2.22 a	0.189 b	0.179 b	8.92 a	59.4 a	29.5 a	43.7 a
Nitrate	2.68 b	0.370 b	2.00 a	0.259 a	0.247 a	6.90 a	54.2 a	23.7 b	25.0 b
Roots:									
Ammonium	2.01 a	0.381 a	1.79 a	1.98 b	0.095 b	14.4 a	232 a	10.2 b	194 b
Nitrate	1.71 a	0.310 a	2.49 a	3.60 a	0.350 a	16.2 a	167 a	16.0 a	390 a

b) Harvest 2

Shoots:									
Ammonium	1.91 a	0.361 a	1.79 a	0.181 b	0.151 b	5.19 a	20.0 a	26.3 a	29.2 a
Nitrate	1.84 a	0.286 b	1.71 a	0.215 a	0.208 a	3.56 b	22.3 a	22.2 b	20.6 b
Roots:									
Ammonium	1.67 a	0.461 a	1.93 b	0.222 b	0.117 b	8.5 b	175 a	10.3 b	196 b
Nitrate	1.44 b	0.335 b	2.37 a	0.488 a	0.352 a	12.6 a	162 a	18.7 a	422 a

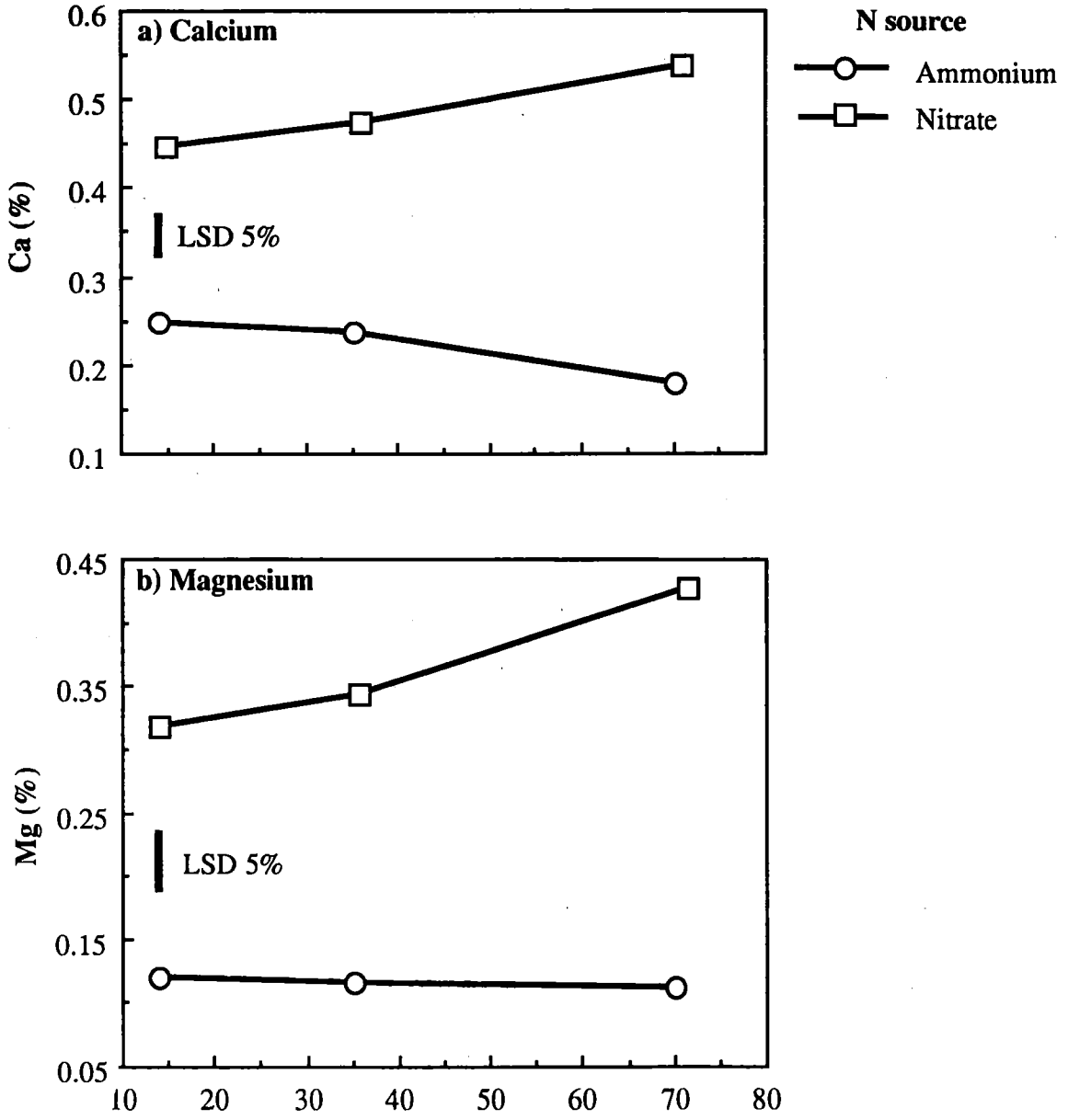

Figure 7.5: Effect of N source and rate on radiata pine seedling root concentrations of a) Ca and b) Mg at harvest 2.

7.3.2.2 Total nutrient uptake

When considering the effect of N source alone it was found that the average total nutrient uptake per pot at harvest 2 (**Table 7.5**) for N, P, K, Cu and B was greater for the ammonium-fed seedlings. The average total amounts of Mg and Fe which were significantly ($p<.05$) higher in the nitrate-fed seedlings. The rate of N addition significantly affected total N ($p<.001$) and Cu ($p=.018$). As the N rate increased from 14 to 35μg ml^{-1} the amount of N uptake pot^{-1} increased (**Figure 7.6**). The interaction between N source and rate was significant ($p=.010$).

The uptake of Cu pot^{-1} increased with increasing N rate.

Table 7.5: Effect of N source on the total uptake of nutrients per pot of radiata pine seedlings at harvest 2. For each nutrient, means followed by the same letter were not significantly different ($p<.05$). The significance of the N source and rate effect on the total uptake of each nutrient are also presented.

	N	P	K	Ca	Mg	Cu	Zn	B	Fe
	--- mg pot^{-1} ---					--- µg pot^{-1} ---			
Ammonium	192 a	38.7 a	184 a	19.1 a	14.6 b	60.4 a	554 a	232 a	675 b
Nitrate	133 b	22.5 b	142 b	21.0 a	18.3 a	41.8 b	403 a	163 b	840 a
N source	<.001	<.001	.001		.009	<.001	.056	.001	.012
N rate	<.001				.051	.018		.064	
N source * rate	.010								

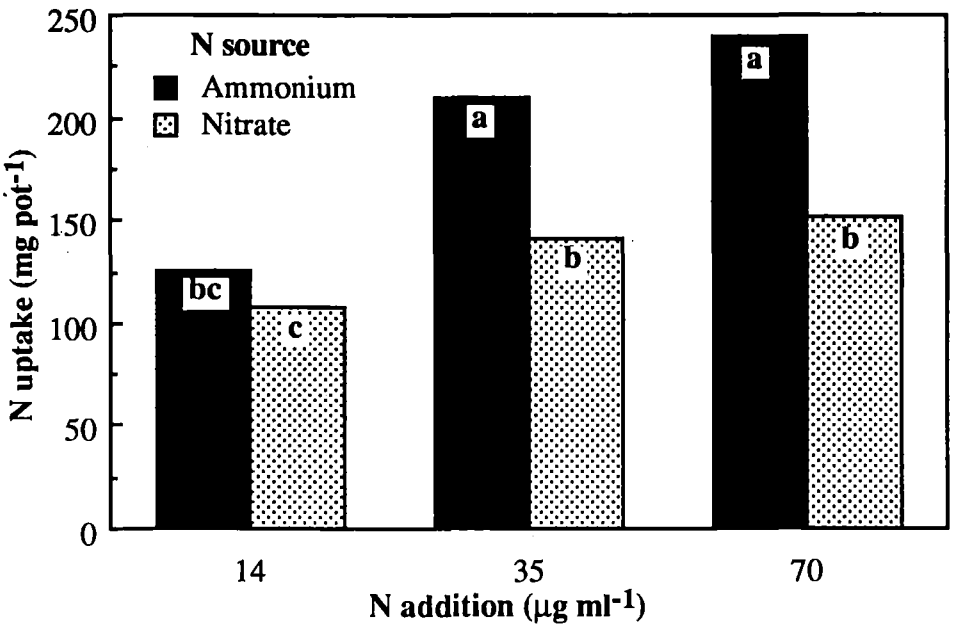

Figure 7.6: Effect of N source and rate on radiata pine N uptake per pot at harvest 2. Means with the same letter were not significantly different ($p<.05$).

7.3.2.3 Partitioning of micronutrients

At harvest 2, the greatest proportions of Cu and B were found in the shoots (**Table 7.6**) of the radiata pine seedlings while Zn and Fe were predominantly in the roots. The source of N significantly ($p<.001$) affected the partitioning of Cu, B and Fe which were all in greater proportions in the shoots of the ammonium-fed seedlings particularly at N rates of N_{35} and N_{70}.

7.4 DISCUSSION

The nutrient solution, added to the radiata pine seedlings during the sand culture pot trial, contained higher concentrations of NH_4, K, Ca, Mg and SO_4 than found in the soil solution by Edmeades *et al* (1985, **Table 7.7**). The sand culture solution concentrations of NO_3, Fe and Mn were within the range of concentrations described in **Table 7.7**. The concentrations of Cu, Zn and B in the sand culture solution were also within the concentration ranges for the soil solution as described by Kabata-Pendias and Pendias (1984, see section 2.4.2).

Table 7.6: Effect of N source and rate on the percentage of micronutrients found in the shoots of radiata pine seedlings at harvest 2. For each nutrient, means with the same letter were not significantly different ($p<.05$).

Micronutrient	N source	N rate (μg ml^{-1}) 14	35	70
		--- % ---		
Cu	Ammonium	58 b	70 a	74 a
	Nitrate	52 bc	53 bc	46 c
Zn	Ammonium	30 a	27 a	34 a
	Nitrate	35 a	32 a	34 a
B	Ammonium	86 b	90 a	92 a
	Nitrate	77 d	82 c	82 c
Fe	Ammonium	25 b	40 a	38 a
	Nitrate	13 d	16 c	15 cd

Table 7.7: Comparison of some major nutrient concentrations in the soil solutions of New Zealand soils (from Edmeades *et al.* 1985) with the concentrations of nutrients added to radiata pine seedlings in the sand culture pot trial solution.

Nutrient	Concentration in the soil solution	--- μg ml^{-1} ---	Concentration in the sand culture solution --- μg ml^{-1} ---
NO_3^-	0.21 - 2.8 mmol L^{-1}	2.9 - 39	14 - 70
NH_4^+	0.09 - 0.39 mmol L^{-1}	1.3 - 5.5	14 - 70
K	0.03 - 1.0 mmol L^{-1}	1.2 - 39	206
Ca	0.34 - 1.2 mmol L^{-1}	14 - 48	60
Mg	0.15 - 0.37 mmol L^{-1}	3.6 - 8.6	50
SO_4^{2-}	0.44 - 0.59 mmol L^{-1}	14 - 19	66 - 227
Fe	2.5 - 45 μmol L^{-1}	0.14 - 2.5	2
Mn	1.5 - 4.6 μmol L^{-1}	0.08 - 0.25	0.13

The rate and particularly the source of N addition affected radiata pine seedling growth and nutrient dynamics. This discussion focuses on the results from the second harvest.

Nitrogen fertilisation has been shown to increase radiata pine biomass on soils of low mineral N status (Nambiar and Fife 1987). This effect can be modified by the source of N - nitrate or ammonium - and radiata pine has been shown to grow better with ammonium-N (Ryan, cited by Tuner and Lambert 1991, McFee and Stone 1968) regardless of the rate of addition (McFee and Stone 1968). However, Adams and Attiwill (1982) found no significant difference in the shoot and root dry weights of nitrate or ammonium-fed seedlings.

By harvest 2 in this study, the ammonium-fed seedlings were significantly heavier (both shoots and roots) and taller than the nitrate-fed seedlings at the N_{70} rate. These results suggest that radiata pine grows better with an ammonium-N source in a controlled environment particularly where N was added at 70μg ml^{-1}.

The effect of N source on seedling size may be related to the extra energy required to reduce nitrate-N to ammonium-N within the plant (Binkley 1986). This may have resulted in the lower N uptake of the nitrate seedlings and, as N uptake was significantly correlated with total seedling weight ($p<.01$) and height ($p<.01$) at harvest 2, the smaller nitrate seedlings. Adams and Attiwill (1982) also noted that N% in the foliage and roots was greatest with the ammonium-N treatment and suggested that the metabolism of absorbed ammonium-N may be faster than nitrate-N.

A relative shift in biomass production from the roots to the shoots can be expected after N fertilisation (Will 1974; cited by Barker 1978). Adams and Attiwill (1982) reported a shoot:root ratio of 1.3 with N added at 42μg ml^{-1} - this value is less than the shoot:root ratios of 2.5 to 4.3 at N_{14} to N_{70} respectively in this experiment. Increasing the rate of N addition increased the shoot biomass, particularly with ammonium, but without a corresponding increase in the root biomass resulted in significantly higher shoot:root ratios. With the provision of full nutrient solutions during the pot trial, this dramatic change in shoot:root ratios did not appear to be a disadvantage to the N_{70} seedlings - particularly those ammonium-fed - by reducing nutrient uptake compared to shoot growth. However, if this same change in shoot:root ratios were to occur in the field it may affect the ability of the tree root system to support its proportionally much larger above-ground biomass as well as reduce the potential exploitation of the soil volume for nutrients. This may be of particular importance for the uptake of micronutrients where the amounts available in the soil are low.

High rates of nitrate-N have been associated with radiata pine stem deformities in agroforestry systems. In this pot trial the height difference, a simple measure of stem deformity, did not indicate any significant difference between ammonium and nitrate, as the source of N, except at N_{14}. The rate of N addition was more significant than the N source and this was particularly noticeable when the height difference increased by a factor of 4 as the rate of nitrate-N addition increased from 14 to 35 and 70μg ml^{-1} (**Table 7.3**). However the height difference for nitrate-N at N_{35} and N_{70} was lower and not significantly different from those at the equivalent rates of ammonium-N addition.

The number of radiata pine trees with stem deformities has been shown to be proportionally higher in trees grown on ex-pasture sites than on land previously in native forest (Hopmans and Flinn 1991). The differences in these two types of planting site were thought to be a function of land use history and its affect on soil fertility which strongly influences the availability of nitrate (Birk 1991). In this pot trial study there was a lot of variation in the height difference data - the coefficient of variation was 103%. However, assuming that the growth of radiata pine seedlings in sand culture reflects the response of radiata pine to increasing inorganic soil N in the field, these results suggest an increase in the amount of nitrate available for uptake may increase the amount of stem deformity measured as seedling height difference (**Table 7.3**).

McFee and Stone (1968) found that large differences in solution N were needed to produce minor changes in plant N concentrations. In this pot trial a five-fold increase in the rate of N resulted in a 33% increase in shoot N concentration, for both N sources, and corresponded to a 54% and 15% increase in N uptake of the ammonium-fed and nitrate-fed shoots respectively.

There were significant differences in both the concentrations and amounts of nutrients in the seedlings according to which source of N had been added. Previous studies have highlighted the effect of N source on the cation-anion balance (e.g. Turner and Lambert 1991) where nitrate stimulates cation uptake and inhibits anion uptake (Haynes 1986a).

Van den Driessche and Dangerfield (1975) found that the Ca concentrations in nitrate-fed seedlings were higher than ammonium-fed seedlings of Douglas-fir (Pseudotsuga mensiezii). In the pot trial study described in this chapter, the concentrations of Ca and Mg were significantly higher in the shoots and roots of the nitrate-fed seedlings and these concentrations increased with increasing N rate. In contrast, the concentrations of Ca, Mg and K declined with increasing rates of ammonium-N in both the shoots and roots indicating that there may be competition between NH_4^+-N and other cations during nutrient uptake. It has been suggested that in situations where ammonium is the N source for plants the K^+ supply could have an inhibitory effect on N uptake (Haynes 1986a). In this experiment K concentrations in the nutrient solutions were the same for each N treatment. The ammonium-fed seedlings had higher K concentrations and a higher total uptake pot^{-1} than the nitrate-fed seedlings.

For the ammonium-fed seedlings it appeared that, as the rate of N addition increased, proportionally more K, Ca and Mg was found in the seedling shoots. Presumably because cation uptake is proportionally less with NH_4^+-N, the plant allocation favours the shoots rather than the roots, and this effect increases with N rate.

In the nitrate-fed roots there was a build up of Cu, Fe, B, Ca and Mg. However, for Cu, B and Fe the root build-up appeared to be to the detriment of their levels in the shoots and indicated that some mechanism was preventing their transport to the shoots. It has been noted that the reduction of nitrate-N to ammonium-N can occur in the roots (Binkley 1986). Adams and Attiwill (1982) detected NRA in the roots, and not the needles, of radiata pine seedlings grown in sand culture, and the NRA increased with increasing rates of nitrate addition.

During the reduction of nitrate a surplus of cations develops which is balanced by the synthesis of organic acid anions (Raven and Smith 1976) such as malate and citrate (Haynes and Goh 1978). For some conifers, nitrate nutrition can result in high levels of organic acids and symptoms of iron deficiency because Fe may be bound to these organic acids which reduces the activity of Fe in the plant (Haynes and Goh 1978). This induced deficiency may also occur for other trace elements (M. Andrews, Pers. comm. 1991).

The inhibition of Fe, and possibly Cu and B, movement to the shoots of the nitrate-fed seedlings may be related to the binding of these trace elements with organic acids. This would reduce their transport to the shoot and increase their storage within the root system. This may account for the different colouration and morphology of the roots of the ammonium and nitrate-fed seedlings. The nitrate-fed roots were darker (**Plate 3a**), regardless of the rate of addition, and appeared to be more finely and numerously branched than the ammonium-fed roots (**Plate 3b**). Previous work has found that greater nitrate availability can result in higher accumulations of Mg, Mn, Fe and Al in the roots not necessarily in proportion to that translocated to the crown (Ryan, cited by Turner and Lambert 1991).

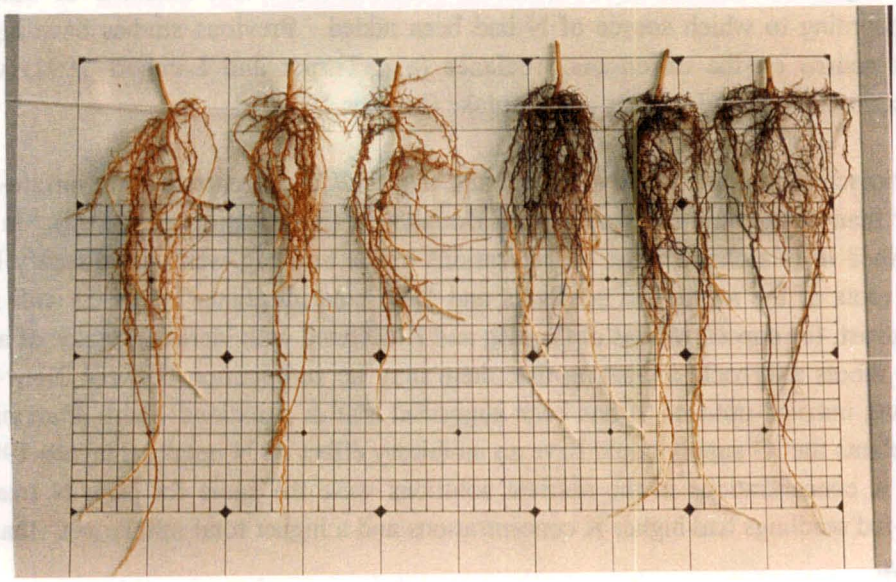

Plate 3a

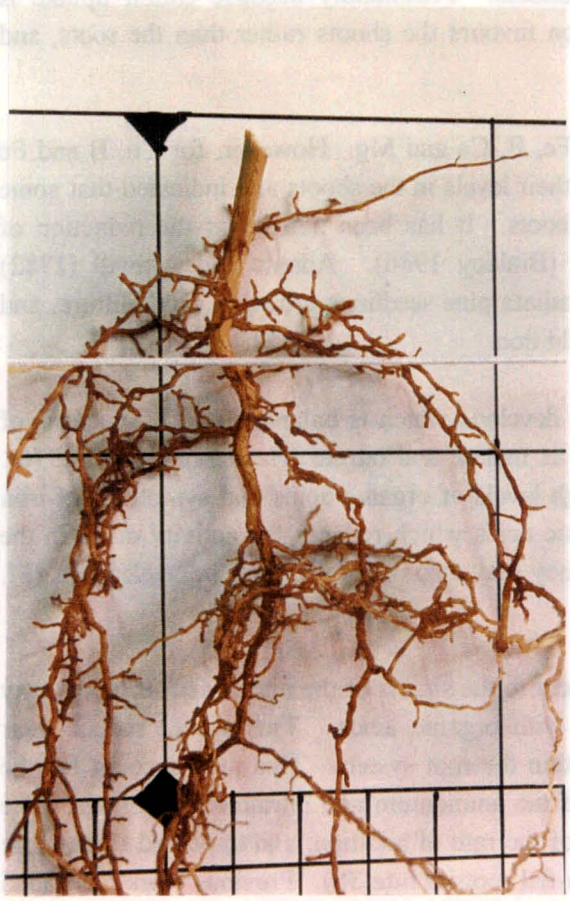

Plate 3b

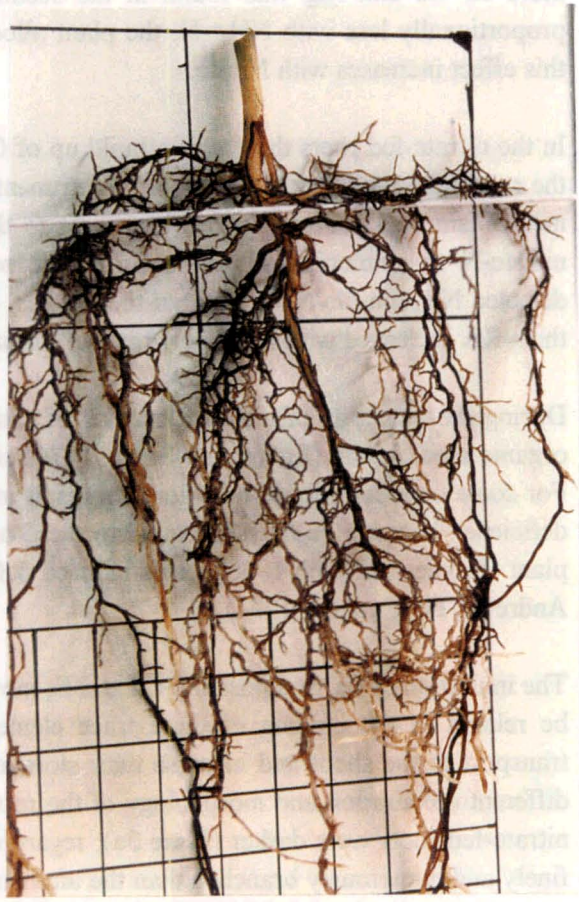

Plate 3c

Plate 3: Effect of the source of N on the a) colour of the root systems of radiata pine seedlings (ammonium-fed roots on the left) and on the colour and morphology of b) ammonium-fed and c) nitrate-fed root systems of radiata pine seedlings grown in sand culture.

The concentrations of both Ca and Mg in the shoots and roots of the nitrate-fed seedlings were higher than those of the ammonium-fed seedlings (**Table 7.4b**). The excess Ca and Mg present in the nitrate-fed roots was not transported to the shoots indicating that the root system may have been acting as a store for these excess cations.

Ammonium-fed seedlings had greater P and B uptake than the nitrate-fed seedlings. Total B was higher in the ammonium-fed plants - most of which was in the shoots - while P in the ammonium-fed seedlings was increasingly transported into the shoots, with higher rates of N, so that the amount of P in the roots declined suggesting that the shift of P from the roots to the shoots was maintaining P concentrations in the shoot. This also occurred in the nitrate-fed seedlings but the P concentrations and uptake were much lower.

7.5 CONCLUSIONS

This pot trial confirmed that both the source and rate of N addition can significantly affect radiata pine seedling nutrition and growth.

From the growth perspective, the addition of ammonium-N had a positive effect on seedling growth but this depended on the rate of addition. For instance, the seedling shoots were heavier when ammonium-N was added at 35 and 70μg ml^{-1} while the roots were heavier with ammonium-N at 14 and 70μg ml^{-1}. Consequently there was no difference between the two N sources on the shoot:root ratio. However, at higher rates of N, the seedlings did grow better when ammonium was the N source.

Nutritionally, there were a number of nutrient measurements that were significantly higher in the ammonium-fed seedlings: the shoot concentrations of P, Cu, B and Fe, the root concentrations of N and P, and the total amount of N, P, K Cu and B in the seedlings. The nutrient measurements that were significantly higher in the nitrate-fed seedlings were: the shoot concentrations of Ca and Mg, the root concentrations of K, Ca, Mg, Cu, B and Fe, and the total amount of Mg and Fe in the seedlings. It appeared that, compared to ammonium-N, the nitrate-N nutrition of radiata pine seedlings promoted the uptake of cations, particularly Ca, Mg and Fe, while reducing the uptake of anions such as P and the shoot concentrations of B.

The proportion of total B and Fe found in the shoots of radiata pine seedlings was higher for all rates of ammonium-N while for Cu it occurred at ammonium-N rates of 35 and 70μg ml^{-1}. The higher proportion of these micronutrients in the ammonium-fed shoots was either a function of higher concentrations in the shoot (Cu and Fe) and/or a greater shoot biomass.

Seedling height difference, a simple measure of stem deformity, was increased with increasing rates of added N. Height differences were higher when the source of N was ammonium rather than nitrate.

These results have implications for the growth of radiata pine on ex-pasture sites where nitrate may be the predominant N source and present at high levels. The cation-anion balance at nutrient uptake may result in less anions, such as P and B, being assimilated. Once ions such as Cu, Fe and B have been taken up into the roots, they may become bound to organic acids, produced during the assimilation of nitrate, and their transport to the shoot significantly reduced.

With the possible increase in the shoot:root ratio at high N levels and the change in root morphology which occurred for nitrate-fed seedlings during this pot trial, the trees ability to absorb nutrients, particularly micronutrients present at low levels in the soil, may be reduced and/or may not meet the demands of fast-growing radiata pine trees.

Chapter 8

The effect of increasing ammonium and boron addition on growth and macro- and micronutrient uptake of Pinus radiata seedlings in two sand culture pot trials differing in the rate of P addition.

8.1 INTRODUCTION

The addition of N (Neilsen *et al* 1992) and P (Flinn *et al* 1979, Mead and Gadgil 1978) fertilisers have been shown to increase radiata pine (Pinus radiata) growth on soils with a low N and/or P status. Ex-pastures, both in New Zealand and Australia, have recently been used as planting sites for radiata pine. The soils of these ex-pasture sites have been characterised as having high N levels and a history of fertiliser additions. The presence or application of high levels of macronutrients such as N, P and K can induce or accentuate micronutrient deficiencies (Hill and Lambert 1981) such as Cu in radiata pine trees (Turvey and Grant 1987, Will 1985) and B (Stone 1990). It also appears that NH_4^+, Ca_2^+, Mg_2^+, and K^+ compete with each other during their accumulation by plants (Haynes and Goh 1978) and high ammonium deposition has been associated with severe imbalances of Mg, K and P relative to N in Scots pine (Pinus sylvestris L.) trees (van Dijk and Roelofs 1988).

A number of recent publications have reported on a variety of growth deformities exhibited by radiata pine growing on ex-pasture sites in Australia and New Zealand (e.g. Birk 1990, Birk *et al* 1991, Boomsma and Hunter 1990, Downes and Turvey 1990, Hunter *et al* 1990, Turvey and Grant 1987, Turvey and Grant 1990). The trees showed higher levels of foliar N and P with possible cation imbalances, limiting micronutrients, and higher levels of some elements such as Al and Mn (Turner and Lambert 1991).

Chapter 7 described the results of a sand culture pot trial, used to identify the effect of ammonium or nitrate as an N source for radiata pine seedling growth, in which increasing rates of NH_4^+-N were added (ie 14, 35 and 70μg N ml^{-1}). The results indicated that increasing the rate of NH_4^+-N from 14 to 35μg ml^{-1} significantly increased shoot dry weights and an increase in N from 14 to 70μg ml^{-1} significantly increased actual seedling height. With increasing NH_4^+-N addition the concentrations of N and Fe in the shoots and the concentrations of N in the roots significantly increased while the concentrations of K and Ca in both the shoots and roots significantly decreased.

The aim of the study described in this chapter was to further investigate the effect of increasing amounts of N and B, on seedling radiata pine at two rates of P. Phosphorus is a macronutrient that can be present at high levels in ex-pasture systems (see Chapter 3) and may influence the micronutrient nutrition of radiata pine.

The study was conducted as two separate sand culture pot trials to avoid the statistical analysis of a three-way interaction between P, N and B. The pot trials were conducted at the same time. The effect of the nutrient treatments was measured in terms of nutrient concentrations and the dry weight of the shoots and roots from which a variety of other nutrient parameters were calculated.

The results will also be discussed in terms of their relevance to radiata pine growing in ex-pasture systems.

8.2 MATERIALS AND METHODS

8.2.1 Sand culture pot trials

The methods and materials for the two ammonium by boron pot trials were the same as those described for the ammonium and nitrate pot trial (Chapter 7) except where otherwise stated below.

From 2 weeks until 2 months of age, all of the radiata pine seedlings in both pot trials were maintained with a nutrient solution containing NH_4^+-N at 7μg ml^{-1}, P at 1μg ml^{-1}, K at 21μg ml^{-1}, Ca and Mg at 5μg ml^{-1} and S at 7μg ml^{-1}. This solution was replaced twice weekly.

At 2 months of age, the seedlings in each pot trial received one of 9 treatments of N and B (**Table 8.1**). The difference between the two pot trials was in the concentration of P which was either 4 μg ml^{-1} (P_4) or 8 μg ml^{-1} (P_8) equivalent to 130μM and 260μM L^{-1} respectively.

Table 8.1: The type and concentration of nutrients added during the P_4 and P_8 sand culture pot trials with radiata pine seedlings.

Nutrient	Rate (μg ml^{-1})	Treatment Number	Compound Type	Other nutrients added (μg ml^{-1})
NH_4^+-N	14	1, 2, 3	$(NH_4)_2SO_4$	S = 16.0
	35	4, 5, 6		40.1
	70	7, 8, 9		80.2
P_4 *	4	1-9	KH_2PO_4	K = 5.0
P_8	8	1-9		10.1
K	195.5	All	K_2SO_4	S = 80.1
Ca	60	All	$CaCl_2.6H_2O$	Cl = 106.2
Mg	50	All	$MgSO_4.7H_2O$	S = 66
Cu	.01	All	$CuCl_2.2H_2O$	Cl = .011
Zn	.01	All	$ZnCl_2$	Cl = .011
B	.1	1, 4, 7	$Na_2B_4O_7.10H_2O$	Na = .106
	.05	2, 5, 8		.053
	.01	3, 6, 9		.011
Mn	.125	All	$MnCl_2.4H_2O$	Cl = .161
Mo	.003	All	$Na_2MoO_4.2H_2O$	Na = .0014
Co	.0012	All	$CoSO_4.7H_2O$	S = .054
Fe	2	All	EDTAFeNa	Na = .82

* The P_4 pot trial consisted of treatments 1 to 9 at a P addition rate of 4μg ml^{-1} while the P_8 pot trial consisted of treatments 1 to 9 at a P addition rate of 8μg ml^{-1}.

There were two harvest dates - one at 2 months (harvest 1) and the other at 4 months (harvest 2) from the beginning of nutrient treatment solution addition.

Physical measurements on the radiata pine seedlings included the number of 'epicorms' and 'branches' per seedling which were measured at harvest 2 (**Figure 8.1**).

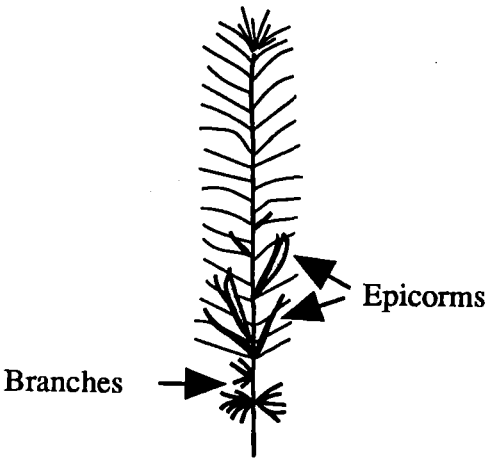

Figure 8.1: Position of branches and epicorms on the radiata pine seedlings grown in the P_4 and P_8 sand culture pot trials.

8.2.2 Calculations

As for the pot trial described in Chapter 7, shoot:root ratios (both harvests) and the total nutrient content of the seedlings pot^{-1} (harvest 2 only) were calculated. Other parameters calculated for both harvests were:

- nutrient:N ratios,

$$\frac{\textit{Macronutrient (mg } g^{-1}\textit{) OR micronutrient (}\mu g\ g^{-1}\textit{)}}{\textit{Nitrogen (mg } g^{-1}\textit{)}}$$

- and the amount of nutrients in the shoots or roots

$$\frac{\textit{Macronutrient \%}}{\textit{100\%}} \times \textit{shoot OR root dry weight (g pot}^{-1}\textit{)}$$

$$\textit{or} \quad \textit{Micronutrient (}\mu g\ g^{-1}\textit{)} \times \textit{shoot OR root dry weight (g pot}^{-1}\textit{)}$$

From the harvest 2 data only the following parameters were also calculated:

- the root efficiency of nutrient uptake,

$$\frac{\textit{Total amount of macro- OR micro-nutrient in the seedling (mg OR }\mu g\ pot^{-1}\textit{)}}{\textit{Root dry weight (g pot}^{-1}\textit{)}}$$

• the percent of the total amount of nutrient in the seedling that was found in the shoots,

$$\frac{\textit{Amount of nutrient in the shoot (g pot}^{-1}\textit{)}}{\textit{Total amount of nutrient in the seedling (g pot}^{-1}\textit{)}} \times 100$$

• and the physiological efficiency of nutrient use as described by Theodorou and Bowen (1993)

$$\frac{\textit{Amount of macro- OR micro-nutrient in the shoot (mg OR } \mu\textit{g pot}^{-1}\textit{)}}{\textit{Shoot dry weight (g pot}^{-1}\textit{)}}$$

8.2.3 Statistics

Data were subjected to analysis of variance (ANOVA) using the computer program GENSTAT. For each harvest (unless otherwise stated) the following effects were examined for each pot trial separately:

(i) The effect of the increasing rates of N and B addition and N by B interactions on seedling shoot and root dry weights, shoot:root ratios, actual seedling height, seedling pot height (harvest 2 only), the number of epicorms seedling^{-1} (harvest 2 only), and the seedling height difference (harvest 2 only).
(ii) The effect of the increasing rates of N and B addition and N by B interactions on the following nutrient characteristics of the shoots and roots per pot: nutrient concentrations, nutrient:N ratios (harvest 2 only) and the amount of nutrients.
(iii) The effect of the increasing rates of N and B addition and N by B interactions on the total amount of nutrient in the seedlings per pot (harvest 2 only), the efficiency of nutrient uptake by the roots (harvest 2 only), the percent of total nutrient and seedling dry weight located in the shoots per pot (harvest 2 only), and the physiological efficiency of nutrient use per pot (harvest 2 only).

The data from the two pot trials was combined so that the effect of the rate of P addition and interactions between P and N or B on the seedling characteristics described in (i) to (iii) above could be analysed in an ANOVA.

The Least Significant Difference (LSD) test was used to compare mean values.

For each pot trial, the linear correlation coefficient (r) was calculated for each of the following paired observations using the computer program STATVIEW:
(i) Shoot nutrient concentrations and shoot dry weights per pot.
(ii) Root nutrient concentrations and root dry weights per pot.
(iii) Shoot concentrations of N and Fe.
(iv) Shoot dry weights and root dry weights per pot.
(v) Total nutrient uptake per pot and root dry weight per pot.
(vi) Total nutrient uptake per pot and total seedling dry weight per pot.
(vii) Nutrient concentrations in the shoots and seedling height difference.
(viii) Shoot B:N ratios and seedling height difference.

8.3 RESULTS

8.3.1 The P_4 pot trial

8.3.1.1 Physical seedling growth

At harvest 1 there was no significant N or B effect on shoot dry weight (which had a mean of 1.56 g pot^{-1}), root dry weight (0.51 g pot^{-1}), shoot:root ratio (3.1), actual seedling height (15.3cm) or the number of epicorms (5.6 $seedling^{-1}$). The addition of N significantly (p=.060) affected the number of branches which significantly (p<.05) increased from 1.3, at N_{14}, to 1.5 and 1.9 branches per seedling for N_{35} and N_{70} respectively.

At harvest 2, the addition of N significantly affected (p<.001) shoot and root dry weights and consequently shoot:root ratios. Shoot dry weights **(Figure 8.2a)** and shoot: root ratios **(Figure 8.2c)** for the N_{14} rate were significantly (p<.05) lower than those at N_{35} and N_{70} while the N_{14} root dry weights were significantly (p<.05) higher than those at N_{70} **(Figure 8.2b)**. The addition of B also had a significant effect on shoot (p=.030) and root (p=.088) dry weights. At both the N_{35} and N_{70} rates, shoot weights were significantly lower in the $B_{.1}$ treatment than the $B_{.01}$ treatment. A similar trend occurred for root dry weights at the N_{35} rate only.

The addition of N significantly affected actual seedling height (p<.001), the number of epicorms per seedling (p<.001), seedling pot height (p=.003) and the number of branches per seedling (p=.023). For pot height, the tallest seedlings, at 26.9cm, occurred in the $N_{35}B_{.01}$ treatment and the shortest seedlings (23.0cm) for the $N_{14}B_{.05}$ treatment. The actual height of the seedlings significantly (p<.05) increased as the rate of N addition increased from 14 to 35μg ml^{-1}**(Figure 8.3)**. As the rate of N addition increased, the number of branches significantly (p<.05) increased from an average of 3.2 $seedling^{-1}$ at N_{14} to 4.0 for the N_{35} and N_{70} rates.

The addition of B was not significant for seedling pot height but was for actual height of the seedlings (p=.056). An increase in B addition from $B_{.01}$ to $B_{.1}$ resulted in a significant decrease in actual seedling height **(Figure 8.3)**. For the other rates of N addition, increasing B had no effect.

The height difference of the seedlings increased as N addition increased from N_{14} to N_{35} **(Figure 8.4)**. The height difference was greatest for the $N_{70}B_{.01}$ treatment, at 2.7cm, and smallest for the $N_{14}B_{.1}$ treatment at 0.8cm. Within each rate of N, increasing B addition did not significantly affect the height difference except at N_{70} where the height difference significantly (p<.05) decreased from $B_{.01}$ and $B_{.05}$.

The number of epicorms per seedling for the N_{14} rate was significantly (p<.05) less than for N_{35} and N_{70} treatments at B rates of 0.01 and 0.05 μg ml^{-1} **(Figure 8.5)**. While the addition of B was significant (p=.071) for the number of epicorms per seedling, within each rate of N increasing B addition did not significantly affect the number of epicorms $seedling^{-1}$.

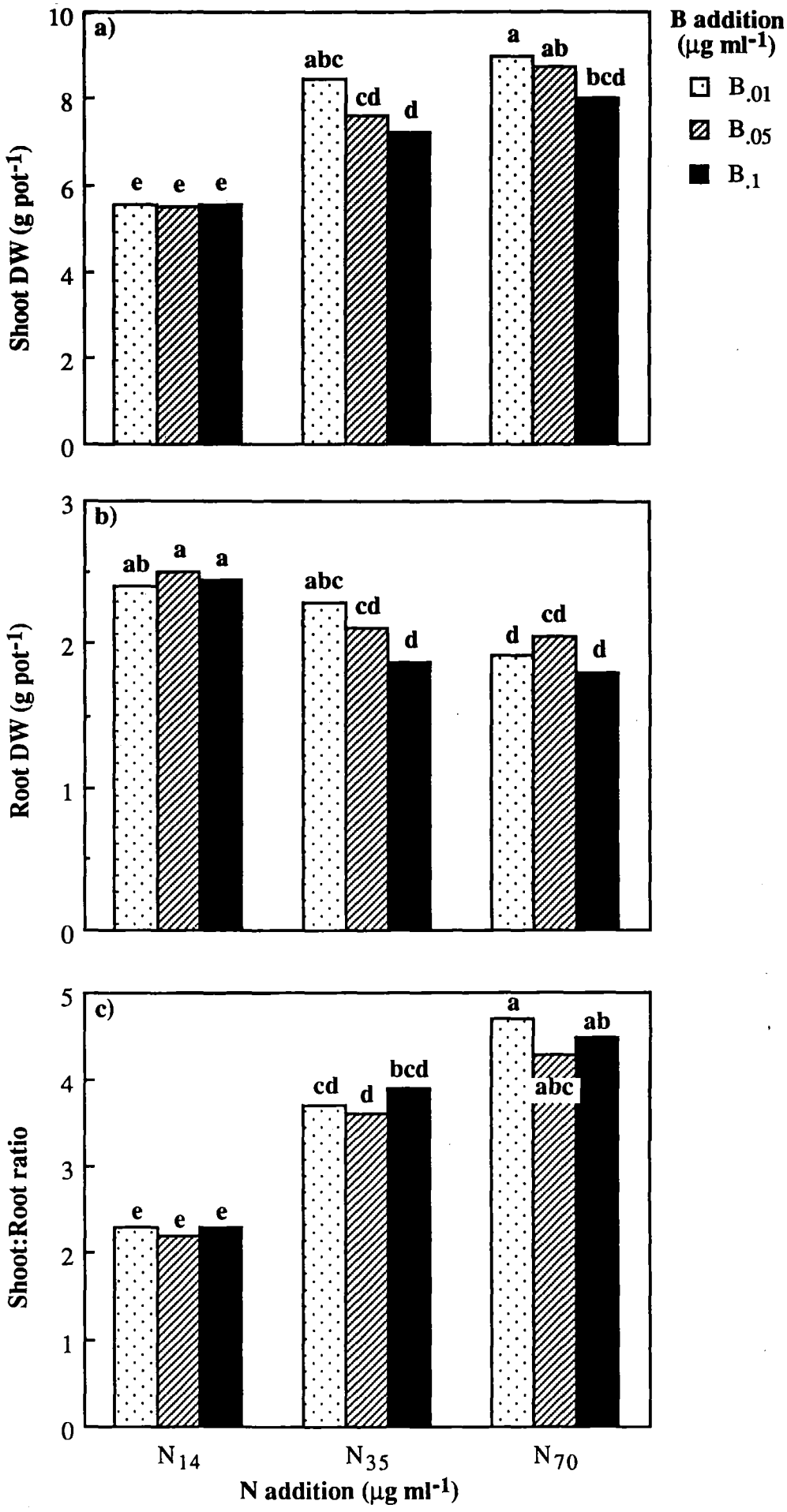

Figure 8.2: Effect of N and B addition on a) shoot dry weight per pot, b) root dry weight per pot and c) shoot:root ratios of radiata pine seedlings at harvest 2 of the P_4 sand culture pot trial. For each physical measurement, means with the same letter were not significantly different ($p<.05$).

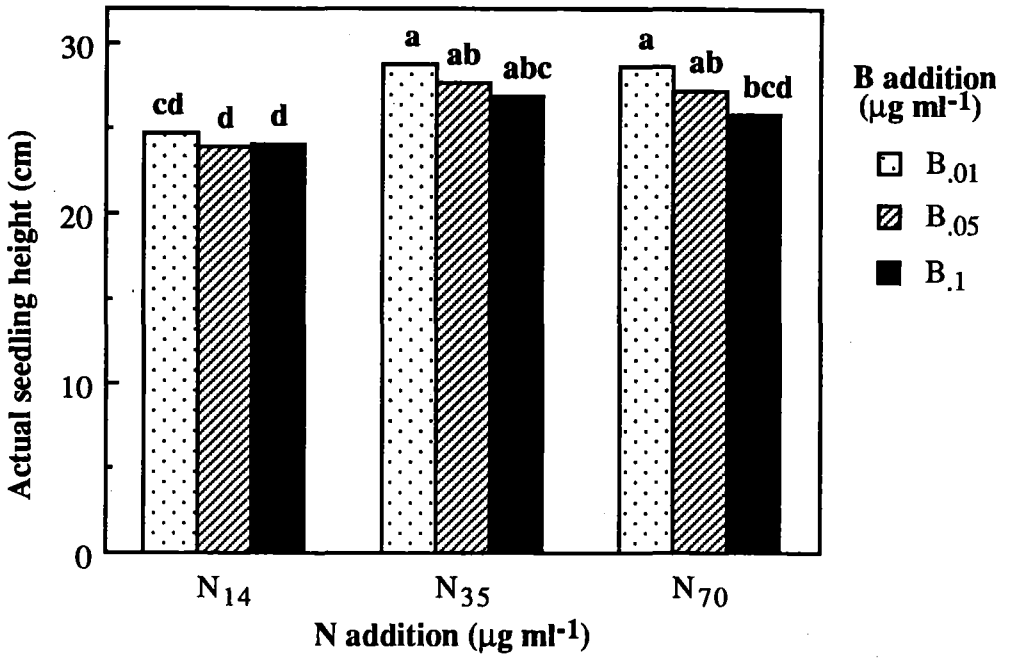

Figure 8.3: Effect of N and B addition on actual radiata pine seedling height at harvest 2 of the P_4 sand culture pot trial. Means with the same letter were not significantly different ($p<.05$).

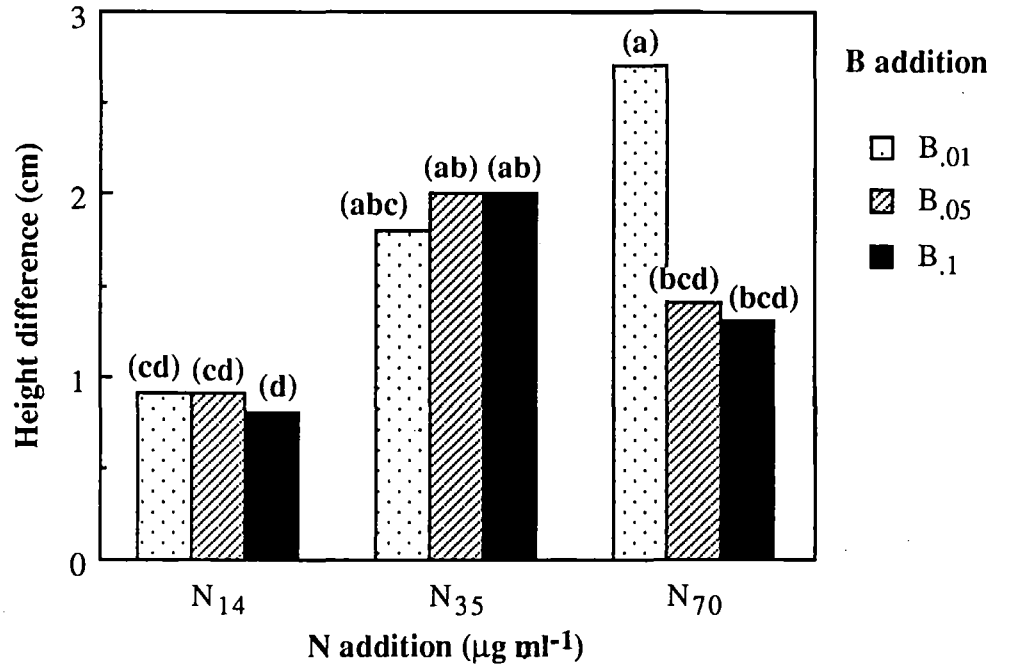

Figure 8.4: Effect of N and B addition on the height difference of radiata pine seedlings at harvest 2 of the P_4 sand culture pot trial. Means with the same letter were not significantly different ($p<.05$) based on means of the transformed data.

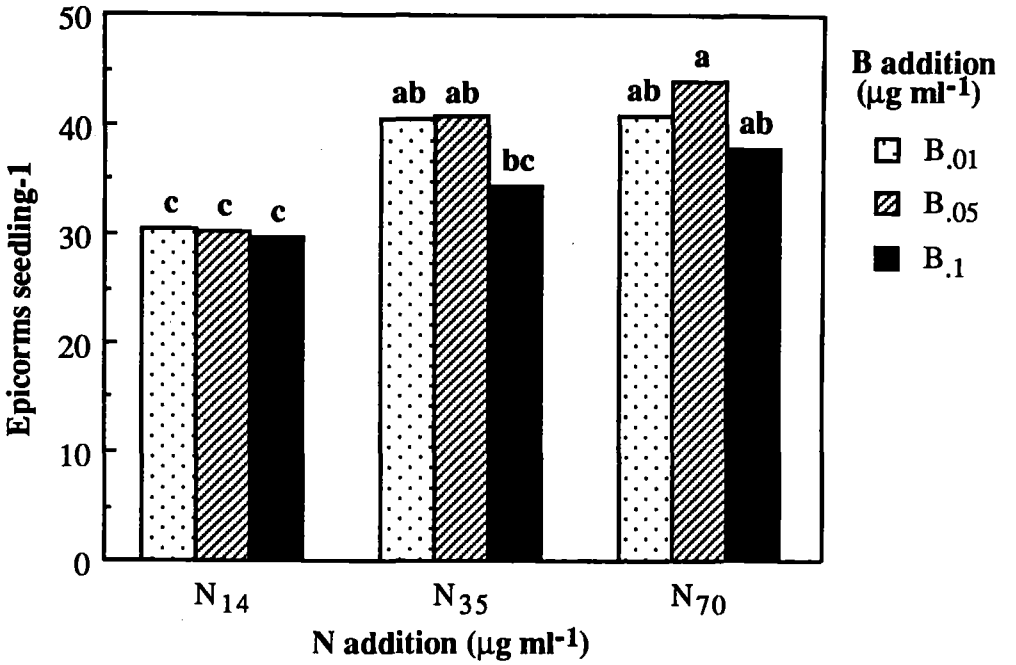

Figure 8.5: Effect of N and B addition on the number of epicorms per radiata pine seedling at harvest 2 of the P_4 sand culture pot trial. Means with the same letter were not significantly different ($p<.05$).

8.3.1.2 Nutrient concentrations

At harvest 1, the addition of N significantly affected the concentrations of N in the shoots ($p<.001$) and the roots ($p=.003$) and the concentrations of Cu in the shoots ($p=.077$) and the roots ($p=.051$). As the rate of N addition increased the concentrations of N significantly increased in the shoots and roots from the N_{14} rate to N_{35} and N_{70} (**Figure 8.6**). The concentration of Cu was significantly ($p<.05$) higher in the shoots of the $N_{35}B_{.1}$ treatment, at 12µg g^{-1}, than in all of the other treatments which had a mean of 9.3µg g^{-1}. In the N_{14} roots, the Cu concentration of 7.6µg g^{-1} was significantly ($p<.05$) less than the 10.9 and 11.1µg g^{-1} recorded for the N_{35} and N_{70} treatments respectively.

Generally, the mean concentrations of Zn and Fe were considerably higher in the roots than the shoots of the radiata pine seedlings at harvest 1, while the concentrations of N, Mg and particularly B were lower in the roots compared to the shoots (**Table 8.2**).

The addition of N had the greatest effect on shoot and, particularly, root nutrient concentrations of the radiata pine seedlings at harvest 2 (**Table 8.3a**). The addition of B only significantly affected the concentrations of B in the shoots and roots (**Table 8.3b**).

Increasing the rate of N from 14 to 35µg ml^{-1} significantly ($p<.05$) increased the shoot concentrations of N while the root concentrations of N significantly increased as the rate of N increased (**Table 8.3a**). For the other nutrients significantly affected by N, increasing N addition resulted in a variety of responses. An increase in N addition from 14 to 70µg ml^{-1} resulted in a significant decrease in the shoot and root concentrations of P and the root concentrations of K. Increasing N addition from 14 to 35µg ml^{-1} resulted in a significant decrease in the root concentrations of Ca and Zn while the shoot concentrations of Ca and Mg decreased with an increase in N from 35 to 70µg ml^{-1}. With increasing N addition the concentrations of Mg and Cu in the roots significantly decreased.

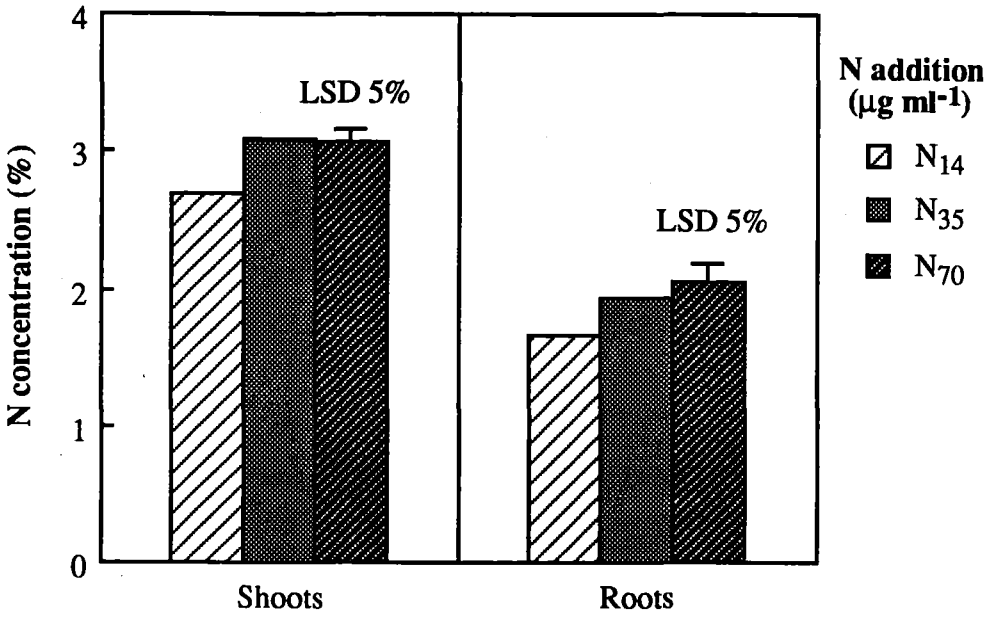

Figure 8.6: Effect of increasing N addition on the concentration of N in the shoots and roots of radiata pine seedlings at harvest 1 of the P_4 sand culture pot trial.

Table 8.2: Mean nutrient concentrations in the shoots and roots of radiata pine seedlings at harvest 1 of the P_4 sand culture pot trial.

	N	P	K	Ca	Mg	Cu	Zn	B	Fe
	--- % ---					--- µg g^{-1} ---			
Shoots	2.95	0.39	2.1	0.191	0.165	9.7	44	27	43
Roots	1.88	0.34	2.0	0.215	0.109	9.9	145	9.9	281

In response to increasing N addition the concentration of Fe behaved differently in the shoots and roots at harvest 2. In the shoots, increasing N addition from 14 to 35µg ml^{-1} significantly ($p<.05$) increased Fe concentrations. In contrast, the concentration of Fe in the roots was significantly higher for the N_{14} treatments than N_{35} and N_{70}.

The B concentrations in the shoots were significantly ($p<.05$) higher for the N_{14} than the N_{35} rate while the root concentrations were not significantly affected by increasing N addition.

In the shoots the B concentrations significantly increased as B addition increased from 0.01 to 0.1µg ml^{-1} while B concentrations in the roots increased with increasing rates of B addition (**Table 8.3b**).

Table 8.3: Effect of increasing rates of a) N and b) B and the probability of a significant N or B main effect (NS = not significant) on the nutrient concentrations of radiata pine seedling shoots and roots at harvest 2 of the P_4 sand culture pot trial. For each nutrient, in shoots or roots, means followed by the same letter were not significantly different ($p<.05$).

a)	N rate (μg ml^{-1})			Probability of N main effect	CV%
	N_{14}	N_{35}	N_{70}		
Shoots:		--- % ---			
N	1.53 b	2.01 a	2.01 a	<.001	13.3
P	0.30 a	0.27 ab	0.24 b	.003	11.2
K	1.69 a	1.69 a	1.64 a	NS	12.5
Ca	0.191 a	0.178 a	0.150 b	.003	12.8
Mg	0.131 ab	0.135 a	0.122 b	.077	9.0
		--- μg g^{-1} ---			
Cu	4.9 a	5.4 a	5.2 a	NS	11.6
Zn	19 a	21 a	19 a	NS	16.6
B	23 a	20 b	21 ab	.090	11.0
Fe	25 b	29 a	30 a	.002	10.4
Roots:		--- % ---			
N	1.28 c	1.50 b	1.92 a	<.001	8.3
P	0.28 a	0.25 ab	0.24 b	.044	10.1
K	1.99 a	1.92 ab	1.62 b	.050	17.1
Ca	0.28 a	0.21 b	0.19 b	<.001	13.3
Mg	0.124 a	0.105 b	0.097 c	<.001	5.8
		--- μg g^{-1} ---			
Cu	9.4 a	8.5 b	6.8 c	<.001	10.0
Zn	155 a	111 b	123 ab	.031	28.9
B	10.8 a	10.5 a	10.2 a	NS	7.5
Fe	218 a	182 b	176 b	.003	12.2

b)	B rate (μg ml^{-1})			Probability of B main effect
	$B_{.01}$	$B_{.05}$	$B_{.1}$	
		--- μg g^{-1} ---		
Shoot B	19.5 b	21.7 ab	22.9 a	.021
Root B	8.5 c	10.5 b	12.4 a	<.001

8.3.1.3 Nutrient:N ratios at harvest 2

The addition of N significantly affected the nutrient:N ratios in the radiata pine seedling shoots and roots at harvest 2 of the P_4 pot trial (**Table 8.4a**). The B:N ratios in the roots were the only nutrient:N ratios significantly affected by B addition (**Table 8.4b**).

Where the rate of N had a significant ($p<.05$) effect on the nutrient:N ratios in the shoots, the N_{14} ratios were significantly higher than in the N_{35} and N_{70} rates (**Table 8.4a**). With increasing N rate the nutrient:N ratios in the roots significantly ($p<.05$) decreased. Only for Zn:N ratios in the roots was there a significant difference between the effect of N_{35} and N_{70}. Root nutrient:N ratios in N_{70} were approximately half those at N_{14}.

Increasing the addition of B from 0.01 to 0.05μg ml^{-1} significantly ($p<.05$) increased root B:N ratios in the roots (**Table 8.4b**).

A comparison of the nutrient:N ratios in the shoots and roots of the radiata pine seedlings showed that the ratios between macronutrients and N were rather similar in both the shoots and the roots with only Ca:N ratios being consistently higher in the roots. In contrast the ratios between the micronutrients Cu, and particularly Zn and Fe, and N were much higher in the roots. The B:N ratios were consistently higher in the shoots.

8.3.1.4 The amount of nutrients in shoots and roots per pot

Generally the increasing addition of N or B had little significant effect on the amount of nutrients found in the shoots and roots of the radiata pine seedlings at harvest 1. The addition of N only significantly affected the shoot amount of N ($p=.010$) and Cu ($p=.048$) and the amount of P ($p=.102$) and K ($p=.095$) in the roots. The amount of N per pot was significantly ($p<.05$) greater in the shoots with the N_{35} and N_{70} rates (49.4 and 47.4 mg pot^{-1} respectively) than for the N_{14} rate (40.9 mg pot^{-1}). The amount of Cu in the shoots was significantly ($p<.05$) higher at N_{35} (17.1 μg pot^{-1}) than at N_{14} and N_{70} (13.8 and 14.1 μg pot^{-1} respectively). In the roots the amount of P and K for the N_{70} rate was 1.51 and 8.2 mg pot^{-1}, respectively, and was significantly ($p<.05$) less than the 1.93 and 11.7 mg pot^{-1} of the N_{14} rate.

At harvest 1, the mean amount of N, P, K, Ca, Mg, Cu and B per pot was higher in the shoots than in the roots (**Table 8.5**). In contrast, the amount of Fe was higher in the roots while the amount of Zn was similar in both the radiata pine seedling shoots and roots.

At harvest 2, N addition had a highly significant effect on the amounts of all the measured nutrients in the shoots and roots of the radiata pine seedlings (**Table 8.6a**). The addition of B was significant for the amount of K and Ca in the shoots and highly significant for the amount of B in the roots (**Table 8.6b**).

In the shoots the amounts of nutrients were significantly ($p<.05$) higher in the N_{35} and N_{70} rates than in N_{14}. For Fe and B in the shoots there was also a significant increase in their amounts from N_{35} to N_{70}.

Table 8.4: Effect of increasing a) N and b) B and the probability of a significant N or B main effect (NS = not significant) on nutrient:N ratios of radiata pine seedling shoots and roots at harvest 2 of the P_4 sand culture pot trial. For each nutrient:N ratio, in the shoots or roots, means followed by the same letter were not significantly different ($p<.05$).

a)	N rate (μg ml^{-1})			Probability of N main effect	CV%
	N_{14}	N_{35}	N_{70}		
Shoots:	--- g macronutrient g^{-1} N ---				
P:N	0.197 a	0.135 b	0.121 b	<.001	10.5
K:N	1.12 a	0.85 b	0.82 b	<.001	16.2
Ca:N	0.127 a	0.089 b	0.075 b	<.001	18.7
Mg:N	0.087 a	0.068 b	0.061 b	<.001	12.1
	--- μg micronutrient g^{-1} N ---				
Cu:N	325 a	270 b	262 b	.006	13.7
Zn:N	1248 a	1031 b	958 b	.020	18.9
B:N	1518 a	1004 b	1067 b	<.001	19.7
Fe:N	1621 a	1457 a	1515 a	NS	15.0
Roots:	--- g macronutrient g^{-1} N ---				
P:N	0.218 a	0.169 b	0.127 c	<.001	12.2
K:N	1.58 a	1.29 b	0.84 c	<.001	20.2
Ca:N	0.216 a	0.139 b	0.098 c	<.001	10.3
Mg:N	0.098 a	0.071 b	0.051 c	<.001	12.3
	--- μg micronutrient g^{-1} N ---				
Cu:N	739 a	570 b	352 c	<.001	16.8
Zn:N	12087 a	7392 b	5863 b	<.001	29.1
B:N	849 a	702 b	530 c	<.001	13.7
Fe:N	17298 a	12239 b	9189 c	<.001	20.8

b)	B rate (μg ml^{-1})			Probability of B main effect
	$B_{.01}$	$B_{.05}$	$B_{.1}$	
Roots:	--- μg micronutrient g^{-1} N ---			
B:N	582 b	707 a	793 a	<.001

Table 8.5: Mean amount of nutrients in the shoots and roots of radiata pine seedlings per pot at harvest 1 of the P_4 sand culture pot trial.

	N	P	K	Ca	Mg	Cu	Zn	B	Fe
	--- mg pot^{-1} ---					--- µg pot^{-1} ---			
Shoots	46	6.1	33	3.0	2.6	15.0	68	42	67
Roots	9.5	1.72	10.1	1.08	0.56	5.0	73	5.0	110

In the roots the amounts of P, K, Mg, Zn, B and Fe were significantly (p<.05) higher in the N_{14} rate than in the N_{70} rate. The amounts of Ca and Cu in the roots significantly increased with increasing N addition. The amount of N in the roots was significantly (p<.05) highest in the N_{70} rate at 37mg pot^{-1} compared to 31mg pot^{-1} for both the N_{35} and N_{70} rates.

Increasing the addition of B from 0.01 to 0.1µg ml^{-1} significantly (p<.05) reduced the amount of K and Ca in the shoots (**Table 8.6b**) while an increase from $B_{.01}$ to $B_{.05}$ resulted in a significant increase in the amount of B in the roots.

8.3.1.5 Total amount of nutrients per pot at harvest 2

The addition of N significantly affected the total amount per pot of N, K, Mg, Cu, Zn, B and Fe in the radiata pine seedlings per pot (**Table 8.7a**). The addition of B significantly affected the total amount per pot of K and Ca (**Table 8.7b**).

The total amounts of N and B increased with increasing rates of N addition. The total amounts of K, Mg, and Cu were significantly higher in the N_{35} and N_{70} rates compared to N_{14}. The total amounts of Zn and Fe in the N_{14} rate were significantly higher than those of the N_{35} and N_{70} rates.

With increasing B addition the total amount of K declined significantly (p<.05) from 172mg pot^{-1} at $B_{.01}$ to 150mg pot^{-1} at $B_{.1}$ (**Table 8.7b**). The total amount of Ca was significantly (p<.05) higher in the $B_{.05}$ rate than the $B_{.1}$ rate.

8.3.1.6 Efficiency of nutrient uptake by the roots at harvest 2

The addition of N significantly affected the root efficiency of N, P, K, Ca, Mg, Cu, B and Fe uptake (**Table 8.8**). With increasing N addition the efficiency of N uptake significantly (p<.05) increased. The efficiency of B uptake was the only other value, apart from N, to significantly increase from N_{35} to N_{70}. For the other nutrients the increase in the efficiency of root uptake was significant from N_{14} to N_{35} only i.e. the efficiency of nutrient uptake at N_{70} was not significantly different from the N_{35} rate. The efficiency of Fe uptake significantly (p<.05) increased from N_{14} to N_{70} while the efficiency of Zn uptake did not significantly change with increasing rates of N addition.

The addition of B was significant (p=.014) for the efficiency of B uptake which significantly (p<.05) increased from 77µg g^{-1} at $B_{.01}$ and 82µg g^{-1} at $B_{.05}$ to 94µg g^{-1} at $B_{.1}$.

Table 8.6: Effect of increasing rates of a) N and b) B and the probability of a significant N or B main effect (NS = not significant) on the amount of nutrient in radiata pine seedling shoots and roots per pot at harvest 2 of the P_4 sand culture pot trial. For each nutrient, in shoots or roots, means followed by the same letter were not significantly different ($p<.05$).

a)	N rate (μg ml^{-1})			Probability of N main effect	CV%
	N_{14}	N_{35}	N_{70}		
Shoots:	--- mg pot^{-1} ---				
N	85 b	155 a	172 a	<.001	14.4
P	16.6 b	20.9 a	20.7 a	.004	13.3
K	94 b	131 a	140 a	<.001	12.7
Ca	10.6 b	13.8 a	12.8 a	.003	14.1
Mg	7.3 b	10.5 a	10.4 a	<.001	13.0
	--- μg pot^{-1} ---				
Cu	27 b	42 a	45 a	<.001	12.5
Zn	106 b	159 a	162 a	<.001	17.8
B	126 c	155 b	181 a	<.001	13.8
Fe	136 c	225 b	256 a	<.001	12.3
Roots:	--- mg pot^{-1} ---				
N	31 b	31 b	37 a	.002	9.8
P	6.8 a	5.3 b	4.7 b	<.001	15.6
K	49 a	40 ab	31 b	.002	22.2
Ca	6.7 a	4.3 b	3.6 c	<.001	11.6
Mg	3.0 a	2.2 b	1.9 b	<.001	12.3
	--- μg pot^{-1} ---				
Cu	23 a	18 b	13 c	<.001	14.3
Zn	383 a	229 b	218 b	<.001	30.9
B	26 a	22 b	20 b	<.001	11.6
Fe	531 a	381 b	340 b	<.001	12.5

8.6 b)	B rate (µg ml^{-1})			Probability of B main effect
	$B_{.01}$	$B_{.05}$	$B_{.1}$	
Shoots:	--- mg pot^{-1} ---			
K	130 a	123 ab	112 b	.087
Ca	13.0 a	13.0 a	11.2 b	.063
Roots:	--- µg pot^{-1} ---			
B	19 b	23 a	25 a	<.001

Table 8.7: Effect of increasing rates of a) N and b) B and the probability of a significant N or B main effect (NS = not significant) on the total amount of nutrients in radiata pine seedlings per pot at harvest 2 of the P_4 sand culture pot trial. For each nutrient, means followed by the same letter were not significantly different (p<.05).

a)	N rate (µg ml^{-1})			Probability of N main effect	CV%
	N_{14}	N_{35}	N_{70}		
	--- mg pot^{-1} ---				
N	116 c	187 b	209 a	<.001	11.8
P	23 a	26 a	25 a	NS	11.5
K	143 b	171 a	171 a	.005	11.1
Ca	17.3 a	18.2 a	16.5 a	NS	11.0
Mg	10.3 b	12.7 a	12.3 a	.005	11.9
	--- µg pot^{-1} ---				
Cu	50 b	59 a	58 a	.012	10.8
Zn	489 a	388 b	380 b	.028	20.7
B	153 c	177 b	201 a	.001	12.8
Fe	667 a	606 b	596 b	.038	9.4

b)	B rate (µg ml^{-1})			Probability of B main effect
	$B_{.01}$	$B_{.05}$	$B_{.1}$	
	--- mg pot^{-1} ---			
K	172 a	164 ab	150 b	.052
Ca	17.9 ab	18.2 a	15.9 b	.038

Table 8.8: Effect of increasing rates of N and the probability of a significant N main effect (NS = not significant) on the amount of nutrient uptake per g of root dry weight of radiata pine seedlings at harvest 2 of the P_4 sand culture pot trial. For each nutrient, means followed by the same letter were not significantly different ($p<.05$).

Nutrient	N rate (µg ml^{-1}) N_{14}	N_{35}	N_{70}	Probability of N main effect	CV%
	--- mg uptake g^{-1} of root ---				
N	48 c	90 b	110 a	<.001	14.1
P	9.6 b	12.6 a	13.4 a	<.001	14.4
K	58 b	82 a	90 a	<.001	13.5
Ca	7.1 b	8.7 a	8.6 a	.003	11.6
Mg	4.2 b	6.1 a	6.5 a	<.001	11.0
	--- µg uptake g^{-1} of root ---				
Cu	21 b	28 a	30 a	<.001	11.2
Zn	199 a	187 a	198 a	NS	18.9
B	63 c	86 b	105 a	<.001	12.9
Fe	274 b	291 ab	311 a	.043	9.8

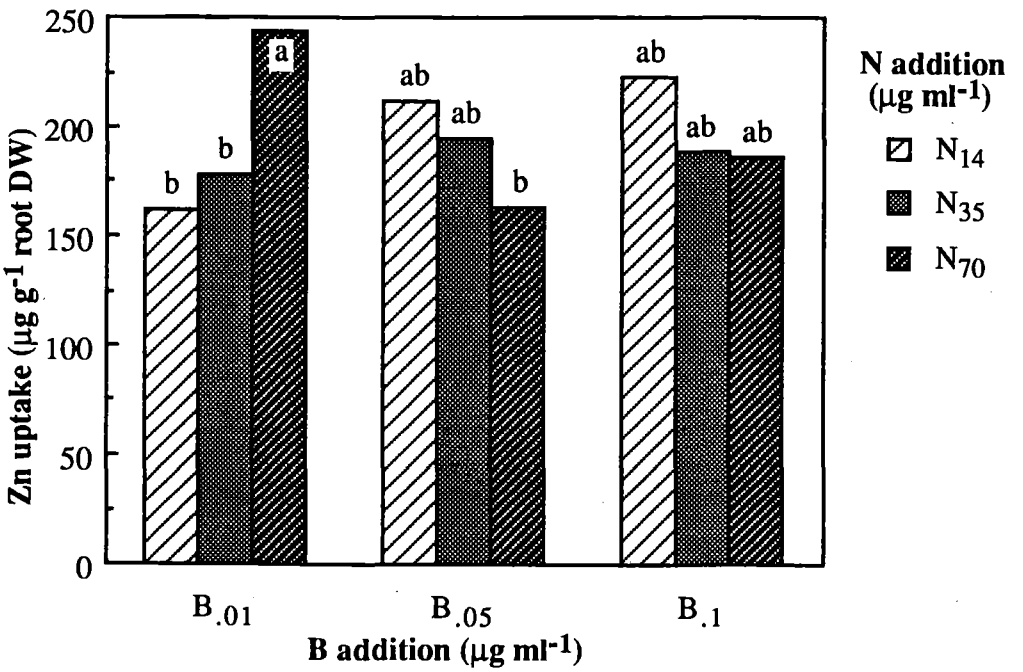

Figure 8.7: Significant interaction ($p=.044$) between the effects of added N and B on the efficiency of Zn uptake by radiata pine seedling roots at harvest 2 of the P_4 sand culture pot trial. Means with the same letter were not significantly different ($p<.05$).

There was a significant interaction between N and B on the efficiency of Zn uptake (**Figure 8.7**, see previous page). Within $B_{.01}$ the application of N_{70} significantly ($p<.05$) increased the root efficiency of Zn uptake compared to N_{14} and N_{35} rates.

8.3.1.7 The percentage of total nutrient per pot located in the shoots at harvest 2

The addition of N significantly affected the percent (%) of total seedling dry weight that was represented by the shoot and the % of total nutrient in the shoots of the radiata pine seedlings (**Table 8.9**). With increasing N addition, the % of total dry weight in the shoot significantly ($p<.05$) increased from 69% at N_{14} to 79% at N_{35} and again to 82% at N_{70}.

With an increase in N rate from 14 to 35μg ml^{-1} there was a significant ($p<.05$) increase in the % of N, P, Ca, and Zn in the shoots. For the % of K, Mg, Cu, B and Fe there was also a significant ($p<.05$) increase from N_{35} to N_{70}.

Increasing the addition of B significantly ($p=.021$) affected the % of B located in the shoots. As the rate of B increased, the % of total B in the shoot declined significantly ($p<.05$) from 88%, at $B_{.01}$, to 86% at $B_{.1}$.

Table 8.9: Effect of increasing rates of N and the probability of a significant N main effect (NS = not significant) on the percentage of total nutrients and total dry weight (DW) found in the shoots of radiata pine seedling shoots at harvest 2 of the P_4 sand culture pot trial. For each nutrient, means followed by the same letter were not significantly different ($p<.05$).

	N rate (μg ml^{-1})			Probability
	N_{14}	N_{35}	N_{70}	of N main effect
	--- % ---			
N	73 b	83 a	82 a	<.001
P	71 b	80 a	81 a	<.001
K	66 c	76 b	82 a	<.001
Ca	61 b	76 a	78 a	<.001
Mg	71 c	83 b	85 a	<.001
Cu	54 c	70 b	77 a	<.001
Zn	23 b	42 a	44 a	<.001
B	83 c	88 b	90 a	<.001
Fe	21 c	37 b	43 a	<.001
DW	69 c	79 b	82 a	<.001

8.3.1.8 Physiological efficiency of nutrient use at harvest 2

The addition of N significantly affected the physiological efficiency in the use of N, P, Ca, Mg, B and Fe (**Table 8.10a**). With increasing N addition from N_{14} to N_{35} the physiological efficiency of N and Fe use significantly ($p<.05$) declined while for P, Ca and Mg it significantly increased from N_{35} to N_{70} and for B from N_{14} to N_{35}.

The addition of B significantly affected the physiological efficiency in the use of B (**Table 8.10b**) which significantly ($p<.05$) decreased as the rate of B addition increased from $B_{.01}$ to $B_{.1}$.

Table 8.10: Effect of increasing rates of a) N and b) B and the probability of a significant N or B main effect (NS = not significant) on the physiological efficiency of nutrient use in radiata pine seedling shoots at harvest 2 of the P_4 sand culture pot trial. For each nutrient, means followed by the same letter were not significantly different ($p<.05$).

a)	N rate (μg ml^{-1})			Probability of N main effect	CV%
	N_{14}	N_{35}	N_{70}		
	--- mg g^{-1} shoot dry weight ---				
N	67 a	50 b	51 b	<.001	14.8
P	337 b	375 b	421 a	.004	12.1
K	60 a	60 a	62 a	NS	13.7
Ca	532 b	569 b	678 a	.004	14.1
Mg	771 ab	747 b	825 a	.076	8.9
	--- μg g^{-1} shoot dry weight ---				
Cu	206 a	189 a	192 a	NS	11.8
Zn	54 a	50 a	54 a	NS	15.9
B	44 b	50 a	48 ab	.102	11.6
Fe	41 a	35 b	33 b	.007	12.6

b)	B rate (μg ml^{-1})			Probability of B main effect
	$B_{.01}$	$B_{.05}$	$B_{.1}$	
	--- μg g^{-1} shoot dry weight ---			
B	52 a	47 ab	44 b	.027

8.3.2 The P_8 pot trial

8.3.2.1 Physical seedling growth

At harvest 1, N addition significantly affected the amount of shoot dry weight per pot ($p=.086$). Considering N addition alone, shoot dry weights increased with increasing rates of N so that the 1.89g pot^{-1} for the N_{70} rate was significantly ($p<.05$) higher than the 1.61g pot^{-1} at the N_{14} rate. Neither N nor B addition had a significant affect on root dry weight per pot which had a mean of 0.52g pot^{-1}.

The addition of N significantly affected the shoot:root ratios ($p<.001$) and the number of epicorms seedling^{-1} ($p=.016$). As the rate of N addition increased the shoot:root ratio significantly ($p<.05$)

increased from 3.0, at N_{14}, to 3.4 and 3.8 at N_{35} and N_{70} respectively. The number of epicorms seedling^{-1} significantly increased from 5.0, at N_{14}, to 6.7 at N_{70}.

At harvest 1, the addition of B significantly affected the number of branches seedling^{-1} (p=.004) which increased from 1.7, at $B_{.01}$, to 2.3 at $B_{.05}$ and then significantly (p<.05) decreased to 1.3 at $B_{.1}$. An interaction between N and B significantly affected the number of branches seedling^{-1} (**Figure 8.8**). In N_{35} rate, B addition at 0.05μg ml^{-1} resulted in an increase in the number of branches seedling^{-1} compared to the $B_{.01}$ and $B_{.1}$ rates. However, for the N_{70} rate increasing B addition from $B_{.01}$ to $B_{.1}$ resulted in a significant reduction in the number of branches seedling^{-1}.

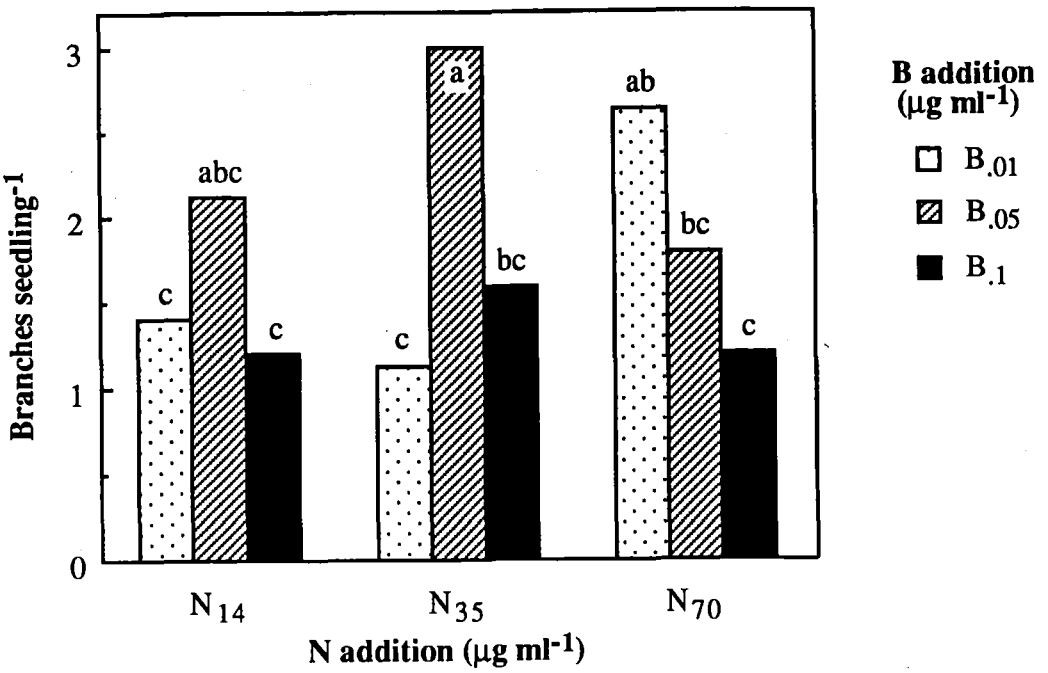

Figure 8.8: Significant interaction (p=.005) between the effects of added N and B on the number of branches per radiata pine seedling at harvest 1 of the P_8 sand culture pot trial. Means with the same letter were not significantly different (p<.05).

By harvest 2, the addition of N significantly affected shoot dry weight pot^{-1} (p<.001), root dry weight pot^{-1} (p=.020), shoot:root ratios (p<.001), actual seedling height (p=.001), the number of epicorms seedling^{-1} (p<.001) and the number of branches seedling^{-1} (p=.029). The addition of B was not significant for any of these seedling physical measurements and there were no significant interactions between N and B.

Shoot dry weights were significantly (p<.05) lower in the N_{14} rate, at an average of 5.9g pot^{-1}, than for the N_{35} and N_{70} treatments at 7.8 and 8.8g pot^{-1} respectively (**Figure 8.9a**). As N addition increased, the average root dry weights decreased significantly from 2.3g pot^{-1} at N_{14} to 1.9g pot^{-1} at N_{35} and N_{70}. However, when considering the effect of B addition as well there were no significant (p<.05) differences between the nine treatments (**Figure 8.9b**). The resulting shoot:root ratios were significantly (p<.05) less in all of the N_{14} treatments than in the N_{35} and N_{70} treatments (**Figure 8.9c**). As N addition increased, the shoot:root ratios nearly doubled from and average of 2.6 at N_{14} to 4.7 at N_{70}.

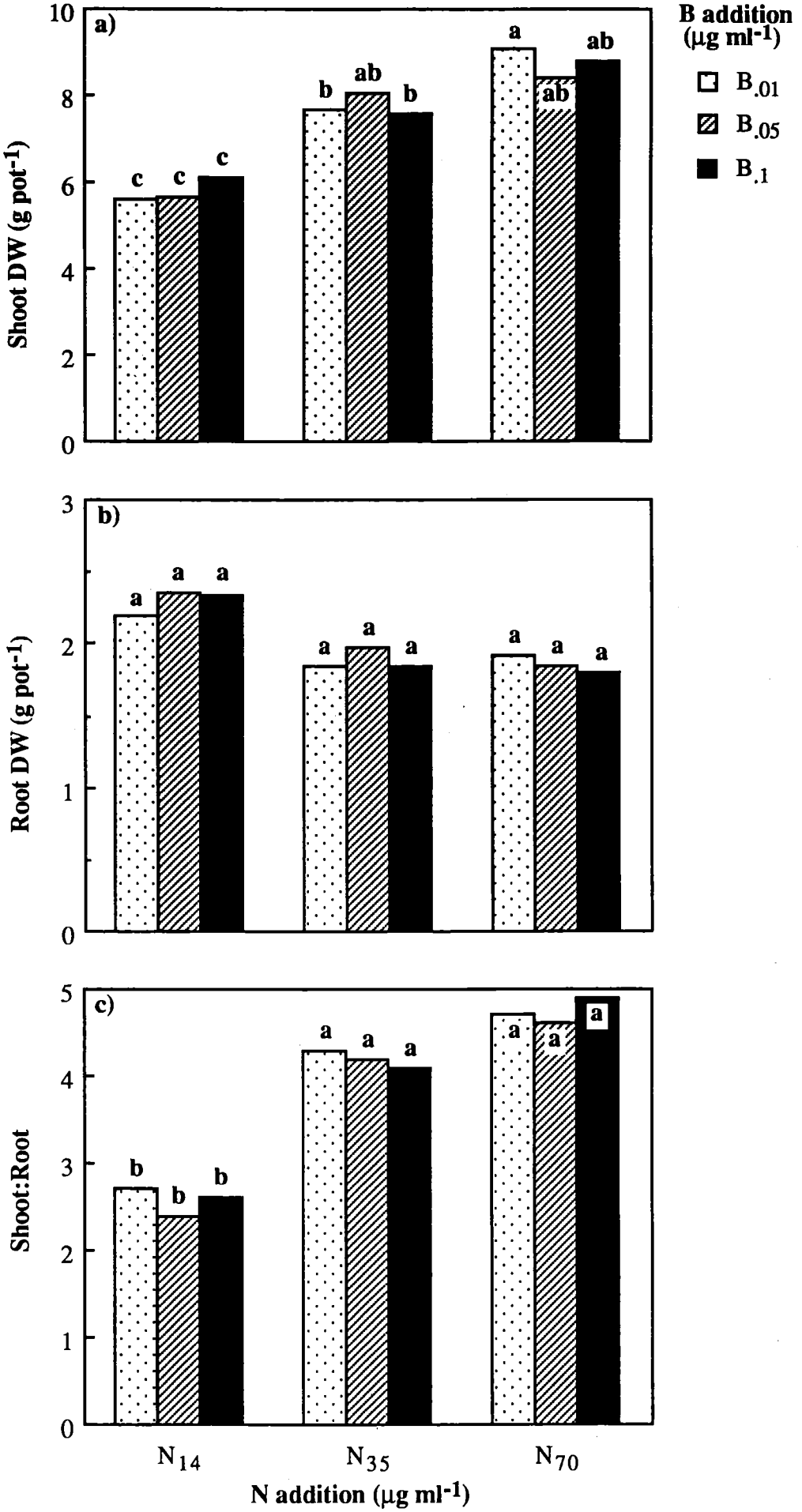

Figure 8.9: Effect of N and B addition on the a) shoot dry weight per pot, b) root dry weight per pot and c) shoot:root ratios of radiata pine seedlings at harvest 2 of the P_8 sand culture pot trial. For each physical measurement, means with the same letter were not significantly different ($p<.05$).

For the effect of N addition alone, actual seedling height was significantly ($p<.05$) greatest at the N_{35} and N_{70} rates with means of 28.3 and 28.8cm respectively, compared to 26.3cm for the N_{14} rate. However when considering B addition as well, there was only a significant difference between the actual seedling heights at $N_{70}B_{.01}$ and $N_{70}B_{.1}$ and those of the N_{14} treatments (**Figure 8.10**).

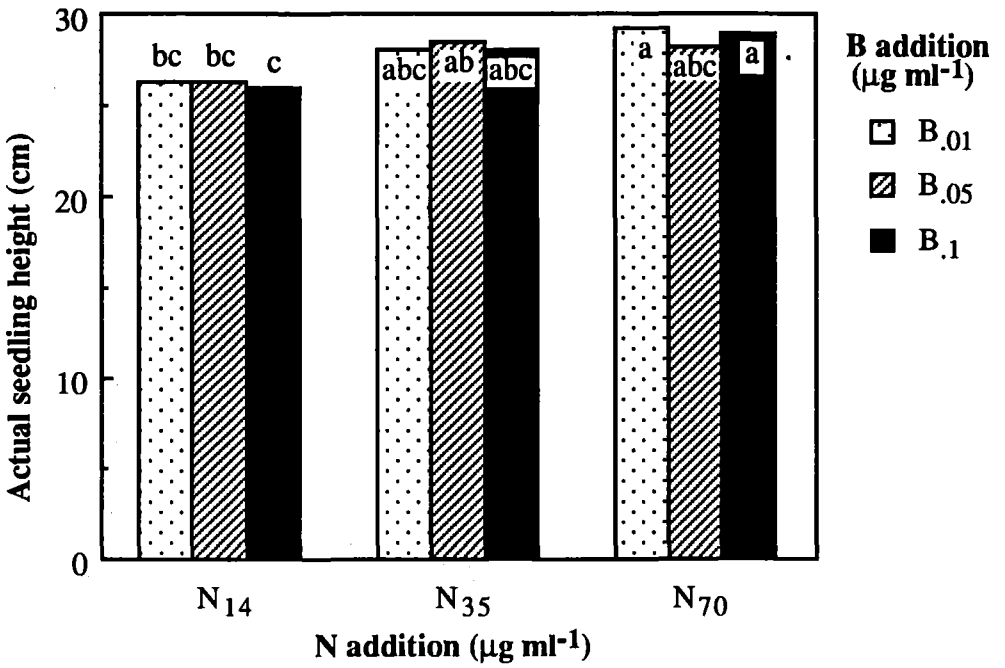

Figure 8.10: Effect of N and B addition on actual radiata pine seedling height at harvest 2 of the P_8 sand culture pot trial. Means with the same letter were not significantly different ($p<.05$).

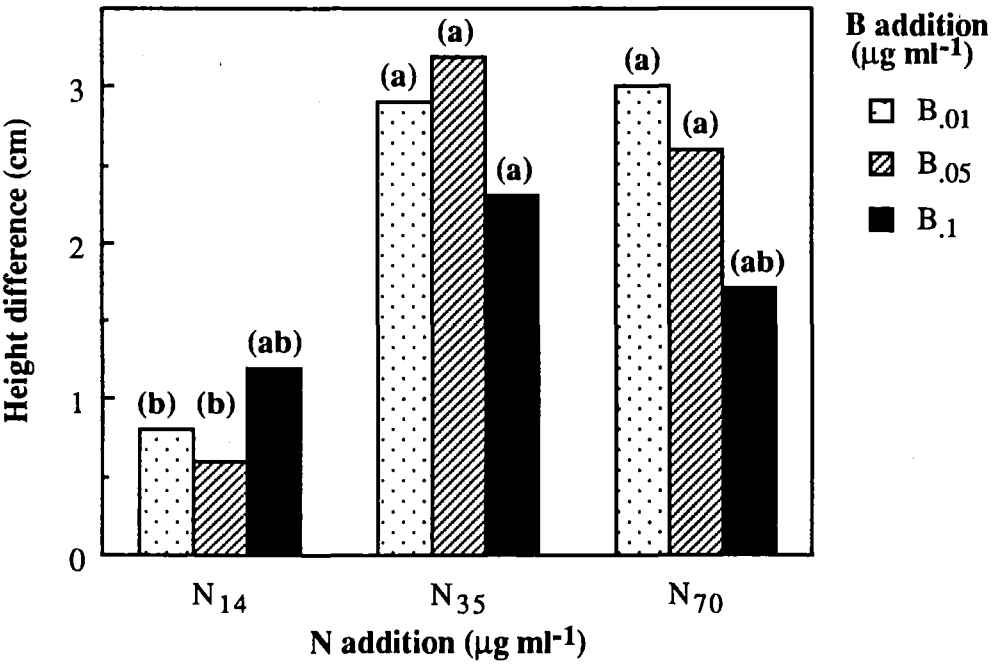

Figure 8.11: Effect of N and B addition on the height difference of radiata pine seedlings at harvest 2 of the P_8 sand culture pot trial. Means with the same letter were not significantly different ($p<.05$) based on the means of the transformed data.

There were significant ($p<.05$) treatment differences in the seedling height differences at harvest 2 (**Figure 8.11**, see previous page) based on means of the transformed data. Considering N addition alone, the height difference increased from 0.95cm at N_{14} to 1.6 and 1.4cm respectively for the N_{35} and N_{70} rates. This effect was modified by the B addition so that the seedling height difference for $N_{14}B_{.1}$ was not significantly different from the N_{35} and N_{70} treatments.

There were significant differences in the number of epicorms seedling^{-1} (**Figure 8.12**). The $N_{70}B_{.01}$ treatment produced more epicorms than any of the N_{14} treatments. The lowest number of epicorms was found for the $N_{14}B_{.05}$ treatment and was significantly less than any of the N_{35} and N_{70} treatments.

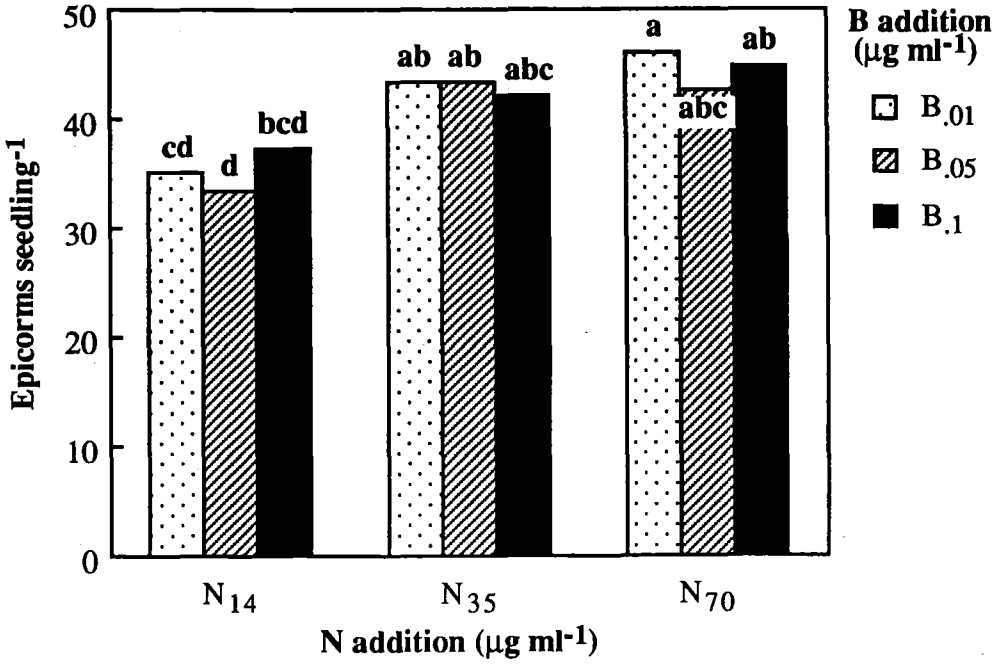

Figure 8.12: Effect of N and B addition on the number of epicorms per radiata pine seedling at harvest 2 of the P_8 pot trial. Means with the same letter were not significantly different ($p<.05$).

The number of branches seedling^{-1} increased significantly ($p<.05$) from 3.2 at N_{14} to 4.0 at N_{35} and then declined to 3.5 at N_{70}.

8.3.2.2 Nutrient concentrations

Both N and B addition had a number of significant effects on nutrient concentrations in the shoots and particularly the roots at harvest 1 (**Table 8.11a**). In the shoots the increasing addition of N significantly ($p<.05$) increased the concentrations of Fe while N concentrations increased from N_{14} to N_{35}. There was a significant decrease in the concentrations of Ca from N_{14} to N_{35}. For the roots, increasing addition of N significantly ($p<.05$) increased the concentrations of N from N_{14} to N_{35} and significantly decreased the concentrations of P and K. The root concentrations of Mg significantly decreased as N addition increased while Ca decreased as N increased from 14 to 70 µg ml^{-1}.

The addition of $B_{.05}$ significantly ($p<.05$) increased the root concentrations of Mg compared to the $B_{.01}$ and $B_{.1}$ rates (**Table 8.11b**). The concentrations of B in the roots were significantly ($p<.05$) greater with $B_{.05}$ and $B_{.1}$ compared to $B_{.01}$.

Table 8.11: Effect of increasing rates of a) N and b) B and the probability of a significant N or B main effect (NS = not significant) on the nutrient concentrations of radiata pine seedling shoots and roots at harvest 1 of the P_8 sand culture pot trial. For each nutrient, in the shoots or roots, means followed by the same letter were not significantly different ($p<.05$).

a)	N rate (µg ml^{-1})			Probability of N main effect	CV%
	N_{14}	N_{35}	N_{70}		
Shoots:		--- % ---			
N	2.47 b	2.92 a	3.01 a	<.001	8.0
P	0.418 a	0.413 a	0.417 a	NS	6.7
K	2.05 a	1.99 a	2.07 a	NS	20.8
Ca	0.198 a	0.174 b	0.174 b	.009	9.0
Mg	0.170 a	0.162 a	0.162 a	NS	7.7
		--- µg g^{-1} ---			
Cu	8.01 a	7.37 a	7.37 a	NS	11.9
Zn	47.4 a	45.6 a	43.3 a	NS	12.9
B	26.3 a	27.1 a	25.8 a	NS	18.8
Fe	33.5 c	38.2 b	42.3 a	<.001	6.5
Roots:		--- % ---			
N	1.67 b	1.99 a	2.12 a	.003	3.7
P	0.46 a	0.42 b	0.44 ab	.021	2.8
K	2.18 a	1.54 b	1.83 ab	.098	14.1
Ca	0.210 a	0.193 ab	0.179 b	.069	5.8
Mg	0.118 a	0.095 b	0.086 c	<.001	2.9
		--- µg g^{-1} ---			
Cu	14.6 a	13.4 a	13.8 a	NS	9.2
Zn	189 a	177 a	155 a	NS	8.9
B	10.1 a	9.5 a	9.3 a	NS	5.9
Fe	246 ab	210 b	265 a	.107	9.8
b)	B rate (µg ml^{-1})			Probability of B main effect	
	$B_{.01}$	$B_{.05}$	$B_{.1}$		
		--- % ---			
Mg	0.094 b	0.107 a	0.098 b	.014	
		--- µg g^{-1} ---			
B	8.5 b	10.0 a	10.4 a	.033	

In general at harvest 1, the concentrations of N, Mg and B were higher in the shoots than in the roots while the concentrations of Cu and especially Zn and Fe were higher in the roots.

The addition of N had a significant effect on the concentrations of nutrients in both the shoots and roots of the radiata pine seedlings at harvest 2 **(Table 8.12a)**. In the shoots, increasing N addition significantly increased the concentrations of N. With an increase in N addition from 14 to 35μg ml^{-1} the concentration of Fe increased while Ca and B decreased. In the roots only the concentrations of N significantly ($p<.05$) increased with increasing rates of N addition while the concentrations of P, Ca and Mg significantly declined. The root concentrations of K significantly ($p<.05$) increased from 1.83 to 2.24% as N addition increased from 14 to 35μg ml^{-1}, and then significantly decreased to 1.38% with the addition of N_{70}. Concentrations of Cu in the roots significantly decreased as N increased from 14 to 35μg ml^{-1} while Fe concentrations significantly increased from N_{35} to N_{70}.

Increasing the addition of B from 0.01 to 0.1μg ml^{-1} significantly increased B concentrations in the shoots. In the roots B concentrations increased with increasing B addition **(Table 8.12b)**.

Increasing the addition of B from 0.01 to 0.1μg ml^{-1} significantly increased Ca concentrations in the roots while Zn concentrations doubled from 77μg g^{-1}, at $B_{.05}$, to 150μg g^{-1} at $B_{.1}$.

The root concentrations of K were significantly affected by an interaction between added N and B **(Figure 8.13)**. Within the N_{14} rate increasing B addition did not significantly affect root K concentrations. For N_{35}, increasing B addition, from 0.01 to 0.1μg ml^{-1}, significantly increased K concentrations. Increasing B addition within the N_{70} rate resulted in a K concentration of 1.61% at $B_{.05}$ which was significantly ($p<.05$) greater than the 1.11% at $B_{.1}$.

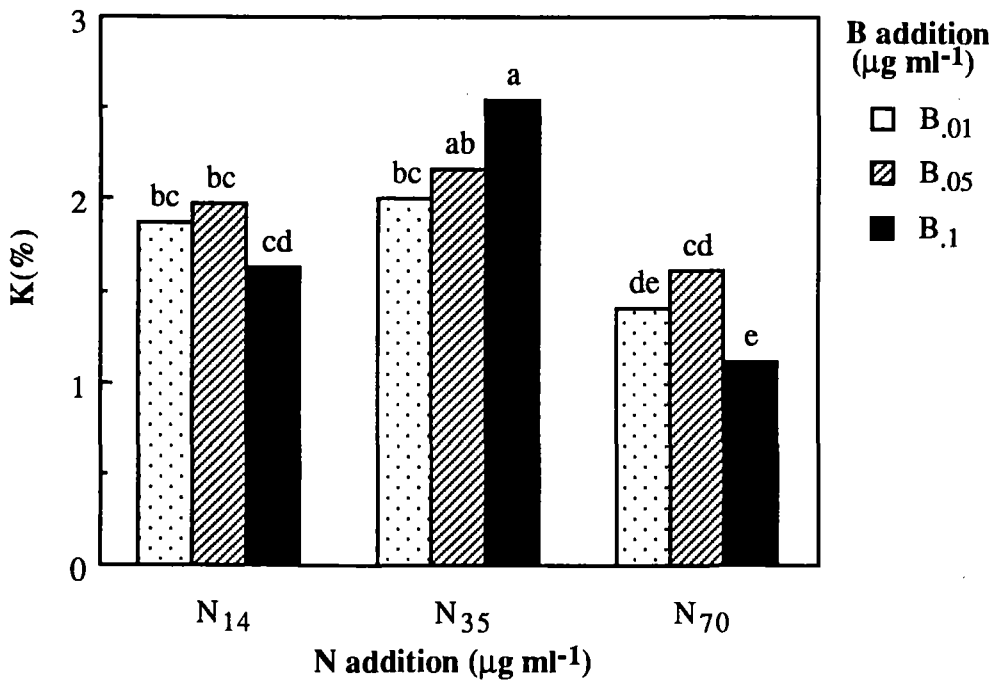

Figure 8.13: Significant interaction between added N and B on the concentration of K in the roots of radiata pine seedlings at harvest 2 of the P_8 sand culture pot trial. Means with the same letter were not significantly different ($p<.05$).

Table 8.12: Effect of increasing rates of a) N and b) B and the probability of a significant N or B main effect (NS = not significant) on the nutrient concentrations of radiata pine seedling shoots and roots at harvest 2 of the P_8 sand culture pot trial. For each nutrient, in shoots or roots, means followed by the same letter were not significantly different ($p<.05$).

a)	N rate (μg ml^{-1})			Probability of N main effect	CV%
	N_{14}	N_{35}	N_{70}		
Shoots:	--- % ---				
N	1.62 c	2.08 b	2.33 a	<.001	4.7
P	0.35 a	0.38 a	0.36 a	NS	10.2
K	1.77 a	1.81 a	1.63 a	NS	15.1
Ca	0.216 a	0.171 b	0.161 b	<.001	10.5
Mg	0.136 a	0.135 a	0.132 a	NS	7.8
	--- μg g^{-1} ---				
Cu	4.2 a	4.9 a	4.5 a	.086	12.8
Zn	21.1 a	19.4 a	18.3 a	NS	14.5
B	23 a	21 b	20 b	.006	8.3
Fe	22 b	28 a	29 a	<.001	8.1
Roots:	--- % ---				
N	1.33 c	1.67 b	1.87 a	<.001	7.2
P	0.48 a	0.43 b	0.38 c	.002	10.2
K	1.83 b	2.24 a	1.38 c	<.001	13.4
Ca	0.266 a	0.214 b	0.161 c	<.001	9.2
Mg	0.125 a	0.113 b	0.097 c	<.001	7.3
	--- μg g^{-1} ---				
Cu	9.9 a	8.1 b	7.4 b	<.001	12.4
Zn	123 a	120 a	106 a	NS	42.6
B	11.2 a	10.7 a	10.4 a	NS	9.6
Fe	192 ab	184 b	211 a	.021	9.7

8.12 b)	B rate (μg ml^{-1})			Probability of B main effect
	$B_{.01}$	$B_{.05}$	$B_{.1}$	
Shoots:	--- μg g^{-1} ---			
B	20 b	22 ab	23 a	.003
Roots:	--- mg g^{-1} ---			
Ca	0.20 b	0.21 ab	0.23 a	.033
	--- μg g^{-1} ---			
Zn	122 ab	77 b	150 a	.021
B	9.0 c	10.6 b	12.6 a	<.001

A comparison between the radiata pine seedling shoots and the roots at harvest 2 showed that the concentrations of macronutrients were similar in both seedling portions. However the concentrations of the micronutrients Cu, and particularly Zn and Fe, were higher in the roots while B concentrations were higher in the shoots.

8.3.2.3 Nutrient:N ratios at harvest 2

The addition of N significantly affected all of the nutrient:N ratios in both the shoots and roots of the radiata pine seedlings (**Table 8.13a**). The addition of B only significantly affected B:N ratios in the shoots and roots and Zn:N and Ca:N ratios in the roots (**Table 8.13b**).

With increasing N addition P:N, K:N, Ca:N, Mg:N, Zn:N and B:N ratios in the shoots and the P:N, Ca:N, Mg:N, Cu:N and Fe:N ratios in the roots significant (p<.05) decreased. As the rate of N increased from 35 to 70μg ml^{-1}, the shoot ratios of Cu:N and Fe:N and the K:N ratios in the roots decreased. The Zn:N and B:N ratios in the roots significantly decreased as N increased from 14 to 70 and 14 to 35μg ml^{-1} respectively.

The B:N ratios in the shoots significantly increased from $B_{.01}$ to $B_{.05}$. B:N ratios in the roots significantly (p<.05) increased with increasing B addition. The Ca:N ratios in the roots significantly increased with an increase in B addition from $B_{.01}$ to $B_{.1}$ while Zn:N ratios significantly increased from 5483 at $B_{.05}$ to 9568 at $B_{.1}$.

8.3.2.4 The amount of nutrients per pot

At harvest 1 the addition of N significantly affected the amount of N (p<.001), Fe (p<.001), P (p=.095) and K (p=.081) in the shoots pot^{-1} and the amount of K (p=.064) and Mg (p=.012) in the roots pot^{-1}. The addition of B on the amount of nutrients in the shoots or roots pot^{-1} was not significant.

As the rate of N addition increased, the amount of N in the shoots significantly (p<.05) increased from 39.3 mg pot^{-1} at N_{14} to 50.8 and 56.9 mg pot^{-1} for N_{35} and N_{70} respectively. The amount of Fe

Table 8.13: Effect of increasing a) N and b) B and the probability of a significant N or B main effect (NS = not significant) on nutrient:N ratios of radiata pine seedling shoots and roots at harvest 2 of the P_8 sand culture pot trial. For each nutrient:N, in the shoots or roots, ratios followed by the same letter were not significantly different ($p<.05$).

a)	N rate (μg ml^{-1})			Probability of N main effect	CV%
	N_{14}	N_{35}	N_{70}		
Shoots:	--- g macronutrient g^{-1} N ---				
P:N	0.218 a	0.181 b	0.156 c	<.001	8.7
K:N	1.01 a	0.87 b	0.70 c	<.001	16.5
Ca:N	0.134 a	0.082 b	0.069 c	<.001	11.0
Mg:N	0.084 a	0.065 b	0.057 c	<.001	7.9
	--- μg micronutrient g^{-1} N ---				
Cu:N	259 a	233 a	191 b	<.001	12.3
Zn:N	1297 a	935 b	788 c	<.001	13.5
B:N	1448 a	1005 b	881 c	<.001	8.7
Fe:N	1373 a	1363 a	1235 b	.011	7.2
Roots:	--- g macronutrient g^{-1} N ---				
P:N	0.37 a	0.26 b	0.21 c	<.001	10.9
K:N	1.40 a	1.35 a	0.74 b	<.001	17.8
Ca:N	0.204 a	0.129 b	0.086 c	<.001	14.7
Mg:N	0.095 a	0.068 b	0.052 c	<.001	11.4
	--- μg micronutrient g^{-1} N ---				
Cu:N	751 a	486 b	398 c	<.001	11.0
Zn:N	9431 a	7322 ab	5706 b	.110	47.1
B:N	850 a	647 b	558 b	<.001	13.2
Fe:N	14549 a	11085 b	11388 c	<.001	12.3
b)	B rate (μg ml^{-1})			Probability of B main effect	
	$B_{.01}$	$B_{.05}$	$B_{.1}$		
Shoots:	--- μg micronutrient g^{-1} N ---				
B:N	1018 b	1119 a	1197 a	.004	
Roots:	--- mg micronutrient g^{-1} N ---				
Ca:N	0.126 b	0.145 ab	0.147 a	.078	
	--- μg micronutrient g^{-1} N ---				
Zn:N	7408 ab	5483 b	9568 a	.075	
B:N	562 c	692 b	801 a	<.001	

significantly ($p<.05$) increased from 54.0 μg pot^{-1}, at N_{14}, to 66.8 μg pot^{-1}, at N_{35}, and again significantly increased to 79.7 μg pot^{-1} at N_{70}.

In the roots the amount of K significantly ($p<.05$) decreased from 11.6 to 8.0 mg pot^{-1} as the rate of N increased from N_{14} to N_{35} respectively. The 9.22mg of K pot^{-1} at N_{70} was not significantly ($p<.05$) different from N_{14} or N_{35}. The amount of Mg also significantly ($p<.05$) decreased from 0.63μg pot^{-1}, at N_{14}, to 0.49 and 0.43μg pot^{-1} for the N_{35} and N_{70} treatments respectively.

The amounts of macronutrients and Cu and B were higher in the shoots than the roots (**Table 8.14**) while the amounts of Zn and particularly Fe were higher in the roots of the radiata pine seedlings at harvest 1.

Table 8.14: Mean amount of nutrients per pot in the shoots or roots of radiata pine seedlings at harvest 1 of the P_8 sand culture pot trial.

	N	P	K	Ca	Mg	Cu	Zn	B	Fe
	--- mg pot^{-1} ---					--- μg pot^{-1} ---			
Shoots	49	7.3	37	3.2	2.9	13.3	79	46	67
Roots	10.0	2.3	9.6	1.01	0.52	7.2	91	5.0	125

At harvest 2 the addition of N was highly significant for the amount of most nutrients in the shoots and roots (**Table 8.15a**) of the radiata pine seedlings while the addition of B significantly affected the amount of B in the shoots and roots and the amount of Zn in the roots (**Table 8.15b**).

In the shoots the amounts of N, P, Mg, B and Fe significantly ($p<.05$) increased as N addition increased. The amounts of K, Cu and Zn increased as the rate of N addition increased from 14 to 35 μg ml^{-1}. In the roots the amounts of Ca significantly ($p<.05$) decreased with increasing N addition. The amounts of P, Mg, Cu, B and Fe in the roots significantly decreased from N_{14} to N_{35} while the amount of K decreased from N_{35} to N_{70}.

The addition of $B_{.05}$ significantly increased the amount of B in the shoots and roots compared to $B_{.01}$. The amount of Zn in the roots pot^{-1} increased as B addition increased from 0.05 to 0.1μg ml^{-1}.

A comparison of the shoots and roots showed that the greatest proportion of N, P, K, Ca, Mg, Cu (at N_{35} and N_{70}) and B were found in the shoots. The roots contained the greatest proportion of Zn and Fe.

8.3.2.5 Total amount of nutrients per pot at harvest 2

The addition of N significantly affected the total amount of macronutrients and B in the radiata pine seedlings pot^{-1} at harvest 2 (**Table 8.16a**). As N addition increased, the total amount of N in the seedlings significantly ($p<.05$) increased - the total amount of N in the seedlings nearly doubled from 125mg pot^{-1} at N_{14} to 237mg pot^{-1} at N_{70}. The the total amount of P, K, Mg and B in the seedlings increased as N addition increased from 14 to 35μg ml^{-1} while the total amount of Ca declined from 18.8 to 16.9mg pot^{-1} as N addition increased from 14 to 70μg ml^{-1}.

Table 8.15: Effect of increasing rates of a) N and b) B and the probability of a significant N or B main effect (NS = not significant) on the amount of nutrient in radiata pine seedling shoots and roots per pot at harvest 2 of the P_8 sand culture pot trial. For each nutrient, in shoots or roots, means followed by the same letter were not significantly different ($p<.05$).

a)	N rate (μg ml^{-1})			Probability of N main effect	CV%
	N_{14}	N_{35}	N_{70}		
Shoots:		— mg pot^{-1} —			
N	95 c	161 b	203 a	<.001	7.9
P	21 d	29 b	32 a	<.001	7.3
K	104 b	139 a	142 a	<.001	15.2
Ca	12.6 a	13.3 a	13.9 a	NS	1.5
Mg	8.0 c	10.4 b	11.5 a	<.001	7.0
		— μg pot^{-1} —			
Cu	25 b	38 a	39 a	<.001	14.5
Zn	123 b	150 a	160 a	.003	13.7
B	138 c	162 b	178 a	<.001	9.2
Fe	131 c	219 b	251 a	<.001	8.7
Roots:		— mg pot^{-1} —			
N	30 a	32 a	35 a	NS	16.4
P	11.1 a	8.0 b	7.1 b	<.001	16.4
K	42 a	42 a	25 b	<.001	18.4
Ca	6.1 a	4.0 b	3.0 c	<.001	18.0
Mg	2.87 a	2.13 b	1.79 b	<.001	17.3
		— μg pot^{-1} —			
Cu	22.8 a	15.2 b	13.5 b	<.001	20.5
Zn	276 a	223 a	195 a	NS	42.3
B	25.4 a	20.4 b	19.2 b	.002	15.5
Fe	441 a	348 b	386 ab	.054	19.3

b)	B rate (μg ml^{-1})			Probability of B main effect
	$B_{.01}$	$B_{.05}$	$B_{.1}$	
Shoots:		— μg pot^{-1} —		
B	146 b	162 a	170 a	.009
Roots:		— μg pot^{-1} —		
Zn	233 ab	158 b	303 a	.021
B	18 b	22 a	25 a	.001

The addition of B significantly affected the total amounts of Zn and B in the seedlings pot^{-1} (**Table 8.16b**). With increasing B addition from 0.01 to 0.05μg ml^{-1} the total amount of B significantly increased. The total amount of Zn significantly increased as B addition increased from $B_{.05}$ to $B_{.1}$.

Table 8.16: Effect of increasing rates of a) N and b) B and the probability of a significant N or B main effect (NS = not significant) on the total amount of nutrients in radiata pine seedlings per pot at harvest 2 of the P_8 sand culture pot trial. For each nutrient, means followed by the same letter were not significantly different (p<.05).

a)	N rate (μg ml^{-1})			Probability of N main effect	CV%
	N_{14}	N_{35}	N_{70}		
	--- mg pot^{-1} ---				
N	125 c	192 b	237 a	<.001	8.1
P	32 b	37 a	39 a	<.001	5.4
K	145 b	182 a	168 a	.008	13.3
Ca	18.8 a	17.2 ab	16.9 b	.092	10.3
Mg	10.9 b	12.5 a	13.3 a	<.001	6.9
	--- μg pot^{-1} ---				
Cu	48 a	53 a	52 a	NS	10.9
Zn	399 a	372 a	354 a	NS	25.4
B	163 b	182 a	197 a	<.001	8.5
Fe	572 a	567 a	638 a	NS	13.3

b)	B rate (μg ml^{-1})			Probability of B main effect
	$B_{.01}$	$B_{.05}$	$B_{.1}$	
	--- μg pot^{-1} ---			
Zn	375 ab	299 b	451 a	.013
B	164 b	184 a	195 a	.002

8.3.2.6 Efficiency of nutrient uptake by the roots at harvest 2

The root efficiency of N, P, K, Mg, Cu, B and Fe uptake was significantly affected by N addition (**Table 8.17**). As the rate of N addition increased the efficiency of N and Fe uptake significantly (p<.05) increased. The efficiency of P, K, Mg, Cu and B uptake significantly (p<.05) increased from N_{14} to N_{35}.

The efficiency of Zn uptake was significantly (p=.021) affected by B addition. As the rate of B increased from $B_{.01}$ the efficiency of Zn uptake decreased from 197 to 150μg g^{-1}, at $B_{.05}$, and then significantly increased (p<.05) to 228μg g^{-1} at $B_{.1}$ which was not significantly different from the value for the $B_{.01}$ rate.

Table 8.17: Effect of increasing rates of N and the probability of a significant N main effect (NS = not significant) on the amount of nutrient uptake per g of root dry weight of radiata pine seedlings at harvest 2 of the P_8 sand culture pot trial. For each nutrient, means followed by the same letter were not significantly different ($p<.05$).

	N rate (μg ml^{-1})			Probability of N main effect	CV%
	N_{14}	N_{35}	N_{70}		
	--- mg uptake g^{-1} of root ---				
N	55 c	104 b	129 a	<.001	12.1
P	14 b	20 a	21 a	<.001	17.4
K	64 b	99 a	91 a	<.001	17.2
Ca	8.3 a	9.3 a	9.2 a	NS	14.3
Mg	4.8 b	6.8 a	7.2 a	<.001	15.8
	--- μg uptake g^{-1} of root ---				
Cu	21 b	29 a	29 a	<.001	15.1
Zn	178 a	202 a	194 a	NS	27.7
B	72 b	99 a	107 a	<.001	16.3
Fe	250 c	303 b	349 a	<.001	8.8

8.3.2.7 The percentage of total nutrients per pot located in the shoots at harvest 2

The proportion of total seedling weight that was represented by the shoot was significantly affected by the addition of N (**Table 8.18**) and increased significantly ($p<.05$) from 72 to 81% as N addition increased from 14 to 35μg ml^{-1}.

The addition of N significantly affected the % of total nutrient in the shoots of the radiata pine seedlings. In the P_8 pot trial the % of N, P, Cu, Zn, B and Fe in the shoots significantly ($p<.05$) increased from N_{14} to N_{35}. The % of K, Ca and Mg significantly increased with increasing N addition.

Only the % of Zn found in the shoots was also significantly ($p=.020$) affected by B addition. As the rate of B addition increased the % of Zn increased significantly ($p<.05$) decreased from 49.5% at $B_{.05}$ to 34.8% for the $B_{.1}$ rate. The % of Zn in the $B_{.1}$ shoots was not significantly different from the 40.1% in the $B_{.01}$ rate.

8.3.2.8 Physiological efficiency of nutrient use at harvest 2

The addition of N was highly significant ($p<.001$) in affecting the physiological efficiency of N, Ca and Fe use and significant for Cu, Zn and B (**Table 8.19a**). As the rate of N addition increased the physiological efficiency of N use decreased. The physiological efficiency of Ca and B use significantly increased from N_{14} to N_{35} while for Zn it increased from N_{14} to N_{70}. The efficiency of Cu and Fe use decreased as N addition increased from 14 to 35μg ml^{-1}.

Table 8.18: Effect of increasing rates of N and the probability of a significant N main effect (NS = not significant) on the percentage of total nutrients and total dry weight (DW) found in the shoots of radiata pine seedling at harvest 2 of the P_8 sand culture pot trial. For each nutrient, means followed by the same letter were not significantly different ($p<.05$).

	N rate (μg ml^{-1})			Probability of N main effect
	N_{14}	N_{35}	N_{70}	
	--- % ---			
N	76 b	84 a	86 a	<.001
P	65 b	78 a	82 a	<.001
K	71 c	77 b	85 a	<.001
Ca	68 c	77 b	82 a	<.001
Mg	74 c	83 b	87 a	<.001
Cu	52 b	71 a	74 a	<.001
Zn	33 b	44 a	48 a	.015
B	84 b	89 a	90 a	<.001
Fe	23 b	39 a	40 a	<.001
DW	72 b	81 a	83 a	<.001

Table 8.19: Effect of increasing rates of a) N and b) B and the probability of a significant N or B main effect (NS = not significant) on the physiological efficiency of nutrient use in radiata pine seedling shoots at harvest 2 of the P_8 sand culture pot trial. For each nutrient, means followed by the same letter were not significantly different ($p<.05$).

a)	N rate (μg ml^{-1})			Probability of N main effect	CV%
	N_{14}	N_{35}	N_{70}		
	--- mg g^{-1} shoot dry weight ---				
N	62 a	48 b	43 c	<.001	5.0
P	285 a	269 a	277 a	NS	10.4
K	56 a	56 a	63 a	NS	16.6
Ca	460 b	594 a	631 a	<.001	11.7
Mg	737 a	745 a	761 a	NS	7.7
	--- μg g^{-1} shoot dry weight ---				
Cu	242 a	209 b	228 ab	.098	13.4
Zn	48 b	52 ab	53 a	.105	13.1
B	43 b	48 a	49 a	.013	9.0
Fe	45 a	35 b	35 b	<.001	9.7

The physiological efficiency of Mg and B use was significantly affected by the rate of B addition (**Table 8.19b**). As the addition of B increased from 0.01 to 0.05μg ml^{-1} the physiological efficiency of Mg and B use significantly ($p<.05$) decreased.

b)	B rate (μg ml^{-1})			Probability
	$B_{.01}$	$B_{.05}$	$B_{.1}$	of B main effect
--- mg g^{-1} shoot dry weight ---				
Mg	783 a	724 b	736 ab	.101
--- μg g^{-1} shoot dry weight ---				
B	52 a	45 b	44 b	.003

8.3.3 Phosphorus

Across the two pot trials it was possible to test for the significance of the two levels of P addition -4 or 8μg ml^{-1} - on the radiata pine seedling growth and nutrient contents and identify any significant interactions between P and N or B additions.

8.3.3.1 Physical seedling growth

The rate of P addition significantly affected shoot dry weights ($p=.003$) and shoot:root ratios ($p=.002$) at harvest 1. The P_8 addition produced significantly ($p<.05$) heavier shoot dry weights and similar root dry weights, compared to P_4, so that the shoot:root ratios were significantly ($p<.05$) higher for the P_8 addition (**Table 8.20**). There was also a significant interaction between P and N addition on harvest 1 shoot:root ratios ($p=.086$) and the number of epicorms $seedling^{-1}$ ($p=.026$). For P_8 addition, shoot:root ratios (**Figure 8.14a**) were significantly promoted by increasing N addition. The number of epicorms $seedling^{-1}$ (**Figure 8.14b**) significantly increased as N addition increased from 14 to 70μg ml^{-1}. In the P_4 pot trial, increasing N addition increased shoot:root ratios - significantly ($p<.05$) from N_{14} to N_{70} - but had no significant effect on the number of epicorms $seedling^{-1}$.

Table 8.20: Effect of P addition on the physical measurements of radiata pine seedlings at harvests 1 and 2 of the P_4 and P_8 sand culture pot trials. Pot height and height difference were not measured at harvest 1. For each harvest and physical measurement, means followed by the same letter were not significantly different ($p<.05$).

		Shoot Dry weight	Root dry weight	Shoot:root ratio
		--- g pot^{-1} ---		
Harvest 1	P_4	1.56 b	0.51 a	3.1 b
	P_8	1.75 a	0.52 a	3.4 a
Harvest 2	P_4	7.3 a	2.2 a	3.5 b
	P_8	7.5 a	2.0 a	3.8 a

Table 8.20 (continued):

		Pot height	Actual height	Height difference	Epicorms	Branches
		--- cm ---			--- No. seedling^{-1} ---	
Harvest 1	P_4	-	15.3 a	-	5.6 a	1.6 a
	P_8	-	15.6 a	-	5.8 a	1.8 a
Harvest 2	P_4	25 b	26 b	1.5 a	37 b	3.7 a
	P_8	26 a	28 a	2.0 a	41 a	3.6 a

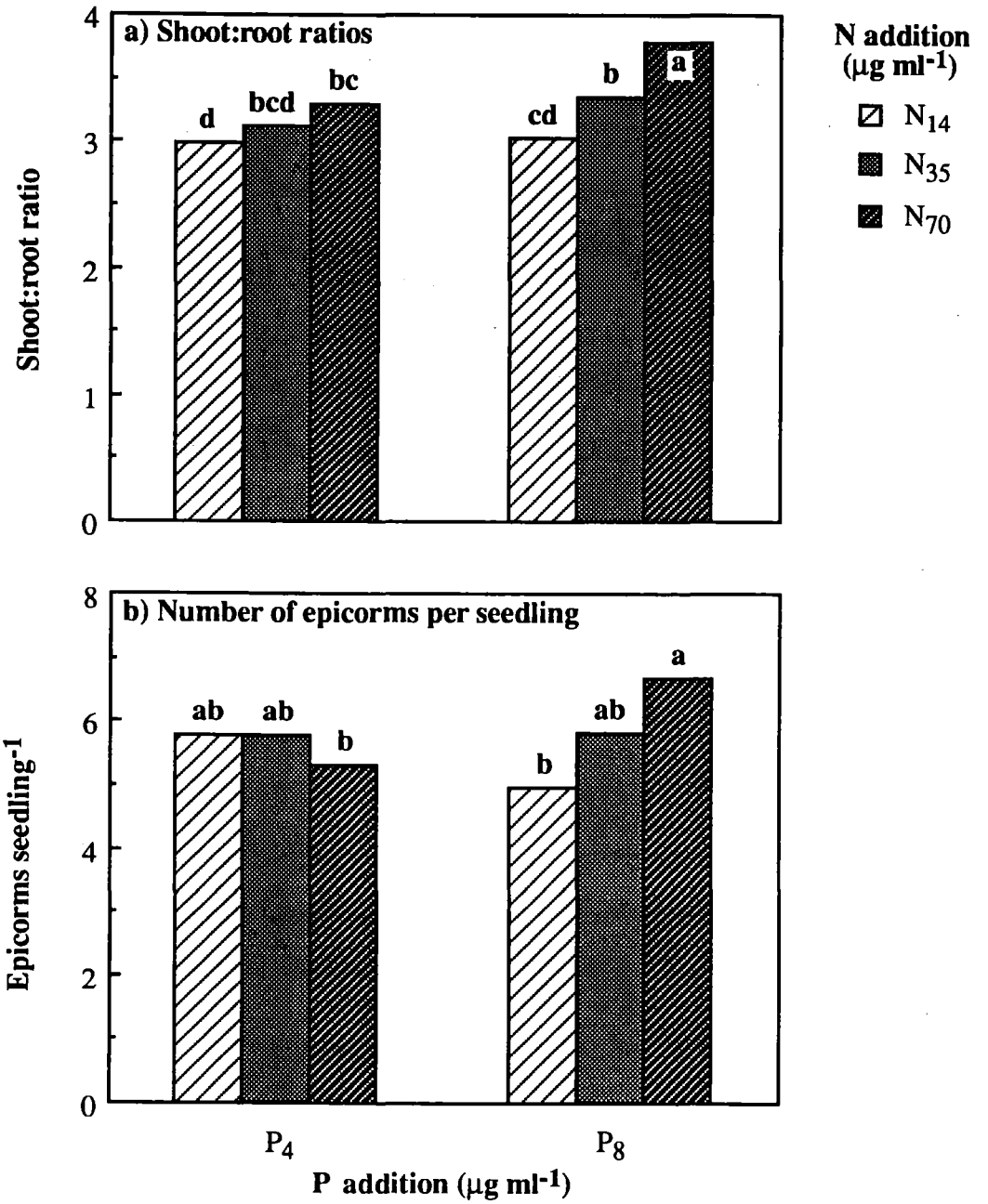

Figure 8.14: Significant interactions between P and N addition on radiata pine seedling physical measurements at harvest 1 of the P_4 and P_8 sand culture pot trials. For each physical measurement, means with the same letter were not significantly different ($p<.05$).

At harvest 2, the rate of P addition significantly affected root dry weights (p=.059), shoot:root ratios (p=.007), seedling pot height (p=.039), actual seedling height (p<.001) and the number of epicorms seedling^{-1} (p<.001). Although there was no significant difference between the effect of P_4 and P_8 on shoot and root dry weights, the resulting shoot:root ratios were significantly (p<.05) higher in the P_8 pot trial. Seedling pot heights, actual seedling heights and the number of epicorms seedling^{-1} were significantly (p<.05) lower with P_4 **(Table 8.20)**. The raw height difference data was skewed. A squareroot transformation of this data was tested in an Anova and indicated that there was no significant difference between the two rates of P.

8.3.3.2 Nutrient concentrations

At harvest 1 the rate of P addition significantly affected the concentrations of N (p=.003), P (p=.008), Cu (p<.001) and Fe (p<.001) in the shoots. The concentrations of N, Cu and Fe were significantly (p<.05) higher in the shoots of the P_4 seedlings while P concentrations were significantly higher for P_8 **(Table 8.21a)**.

There was a significant interaction between P and N addition on the shoot concentrations of Cu (p=.037) and Fe (p=.007) at harvest 1. At the P_4 rate, the addition of N_{35} significantly (p<.05) promoted shoot Cu concentrations above the N_{14} and N_{70} rates **(Figure 8.15a)**. For P_8 there was no significant difference between the three rates of N. For the Fe concentrations, there were no significant differences between the three rates of N in the P_4 treatment **(Figure 8.15b)** but with increasing N addition in the P_8 pot trial, the concentration of Fe significantly (p<.05) increased from 33.5μg g^{-1}, at N_{14}, to 38.2μg g^{-1}, at N_{35}, and again to 42.3 μg g^{-1} at N_{70}.

In the roots at harvest 1 the rate of P addition significantly affected the concentrations of N (p=.090), P (p<.001), Ca (p=.037), Mg (p=.047), Cu (p<.001) and Zn (p=.007). The concentrations of P, Cu and Zn were significantly (p<.05) higher in the P_8 pot trial while Ca was significantly (p<.05) higher for P_4 **(Table 8.21a)**. There were no significant interactions between P and N or B on the root concentrations of nutrients at harvest 1.

At harvest 2 the rate of P addition significantly affected the shoot concentrations of N (p=.004), P (p<.001), Cu (p<.001) and Fe (p=.045). The concentrations of Cu and Fe were significantly (p<.05) higher for P_4 while the concentration of N and P were significantly greater for the P_8 rate **(Table 8.21b)**.

The interaction between P and N addition was significant (p=.016) for the shoot concentrations of P at harvest 2. With P_8 the increasing addition of N had no significant effect on P concentrations **(Figure 8.16)**. For P_4 the concentration of P significantly (p<.05) declined from 0.30% at N_{14} to 0.24% at N_{70}.

Table 8.21: Effect of P addition on the nutrient concentrations in the shoots and roots of radiata pine seedlings at two harvests of the P_4 and P_8 sand culture pot trials. For each nutrient in the shoots or roots, means followed by the same letter were not significantly different ($p<.05$).

a) Harvest 1

		N	P	K	Ca	Mg	Cu	Zn	B	Fe
		--- % ---					--- µg g^{-1} ---			
Shoots	P_4	3.0 a	0.39 b	2.11 a	0.191 a	0.165 a	9.7 a	44 a	27 a	43 a
	P_8	2.8 b	0.42 a	2.04 a	0.182 a	0.165 a	7.6 b	46 a	26 a	38 b
Roots	P_4	1.88 a	0.34 b	2.00 a	0.215 a	0.109 a	9.9 b	145 b	9.9 a	218 a
	P_8	1.93 a	0.44 a	1.85 a	0.194 b	0.100 a	13.9 a	174 a	9.6 a	241 a

b) Harvest 2

		N	P	K	Ca	Mg	Cu	Zn	B	Fe
		--- % ---					--- µg g^{-1} ---			
Shoots:	P_4	1.85 b	0.270 b	1.67 a	0.173 a	0.129 a	5.2 a	19.5 a	21 a	28 a
	P_8	2.01 a	0.364 a	1.74 a	0.183 a	0.134 a	4.5 b	19.6 a	22 a	26 b
Roots:	P_4	1.57 a	0.258 b	1.84 a	0.22 a	0.109 a	8.2 a	126 a	10.5 a	67 a
	P_8	1.62 a	0.431 a	1.84 a	0.21 a	0.112 a	8.5 a	116 a	10.8 a	67 a

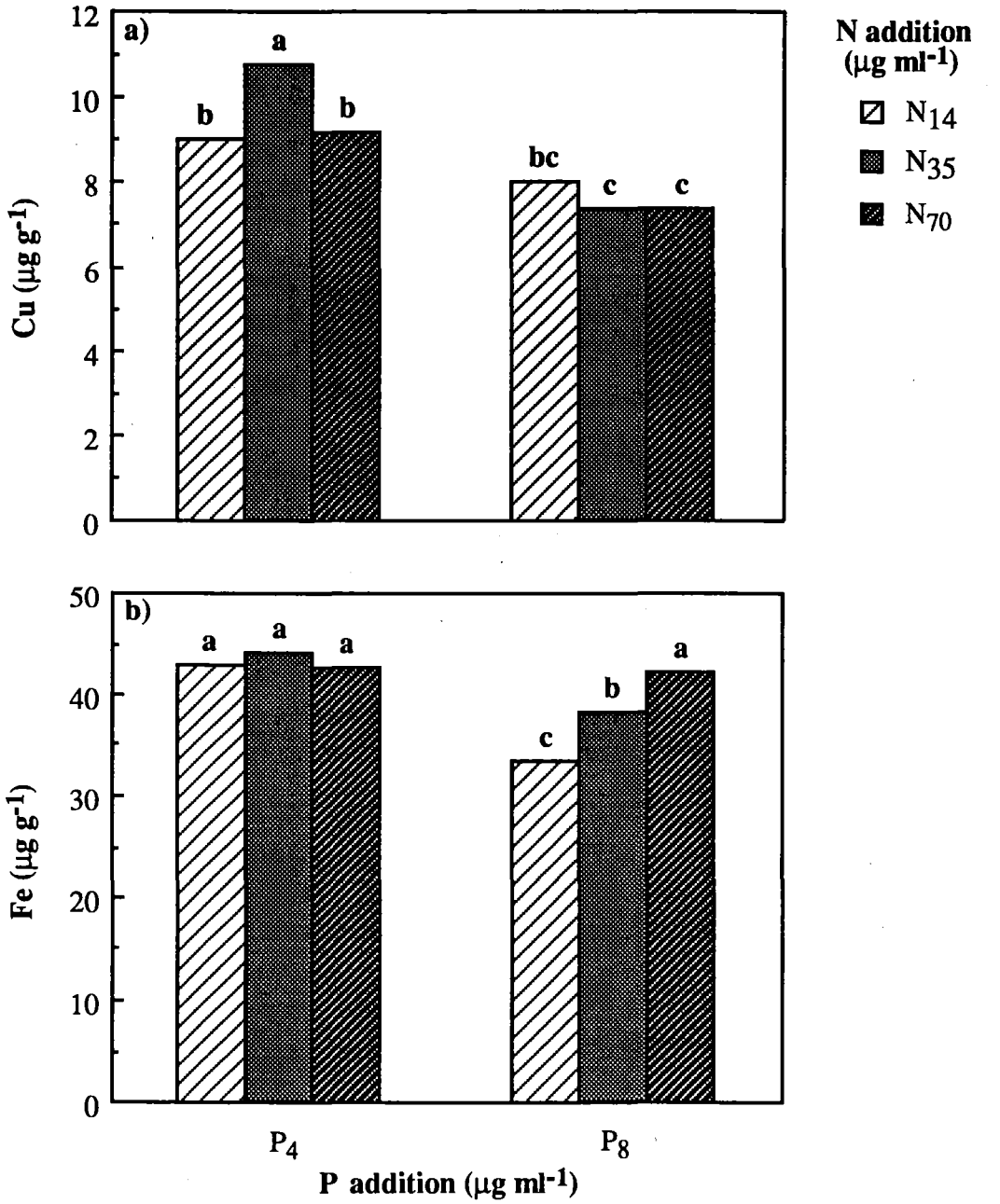

Figure 8.15: Significant interactions between P and N addition on the shoot concentrations of a) Cu and b) Fe of radiata pine seedlings at harvest 1 of the P_4 and P_8 sand culture pot trials. For each nutrient, means with the same letter were not significantly different ($p<.05$).

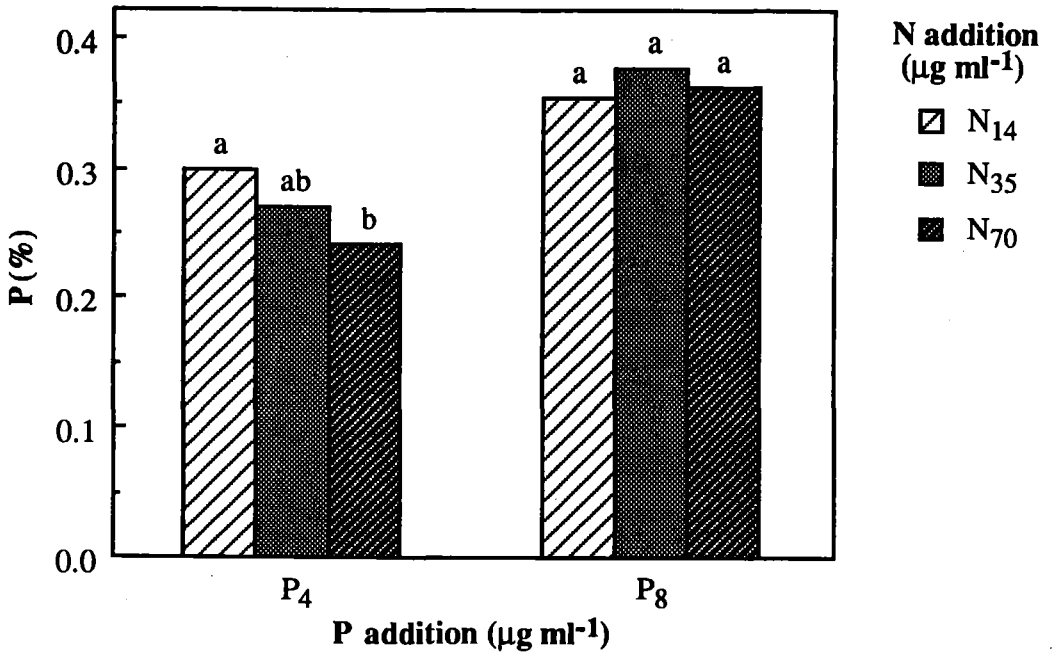

Figure 8.16: Significant interaction between P and N addition on the shoot concentrations of P in radiata pine seedlings at harvest 2 of the P_4 and P_8 sand culture pot trials. Means with the same letter were not significantly different ($p<.05$).

The rate of P addition was significant for the harvest 2 root concentrations of P ($p<.001$) and Ca ($p=.083$). The P concentrations were significantly ($p<.05$) higher for the P_8 addition (**Table 8.21b**).

There was a significant interaction between P and N addition for the root concentrations of N ($p=.033$), P ($p=.029$), K ($p=.011$), Ca ($p=.086$), Zn ($p=.061$) and Fe ($p<.001$). Within both the P_4 and P_8 pot trials the root concentration of N increased significantly ($p<.05$) with increasing N addition (**Figure 8.17a**). In the P_4 pot trial the greatest increase in N resulted from N_{35} to N_{70} while for P_8 it occurred from N_{14} to N_{35}.
For P_4, there was no significant ($p<.05$) effect of increasing N addition on the root P concentrations (**Figure 8.17b**). At P_8, increasing N addition significantly ($p<.05$) decreased P concentrations.

Within the P_4 addition, the root concentrations of K significantly ($p<.05$) decreased as N addition increased from N_{14} to N_{70} (**Figure 8.17c**). In the P_8 rate, K concentrations significantly increased from N_{14} (1.83%) to N_{35} (2.24%) and then significantly decreased to 1.38% at N_{70}.

The Ca concentrations significantly ($p<.05$) declined with increasing N addition particularly in the P_8 pot trial (**Figure 8.17d**). For P_4, there was a significant decrease in Ca from N_{14} and N_{35}.

There was no significant ($p<.05$) difference between the three rates of N on Zn concentrations in the P_4 pot trial (**Figure 8.17e**). However, for P_8 the addition of N_{35} resulted in a Zn concentration significantly lower than that for N_{14} and N_{70}.

With increasing N addition in the P_4 rate, Fe concentrations declined significantly ($p<.05$) from N_{14} to N_{35} (**Figure 8.17f**). For P_8, Fe concentrations significantly increased from N_{35} and N_{70}.

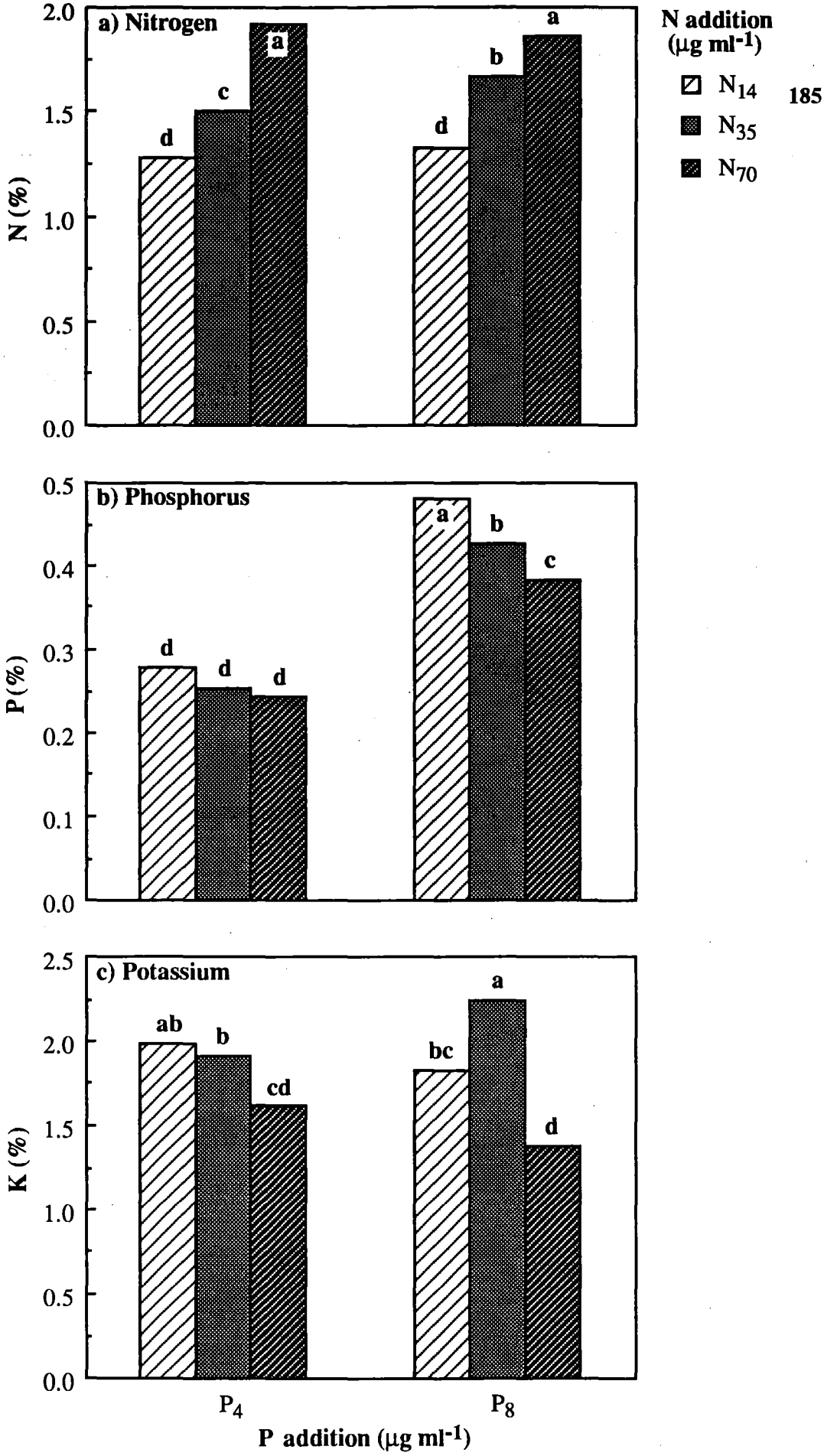

Figure 8.17: Significant interactions between P and N addition on the root concentrations of nutrients in radiata pine seedlings at harvest 2 of the P_4 and P_8 sand culture pot trials. Means with the same letter were not significantly different ($p<.05$).

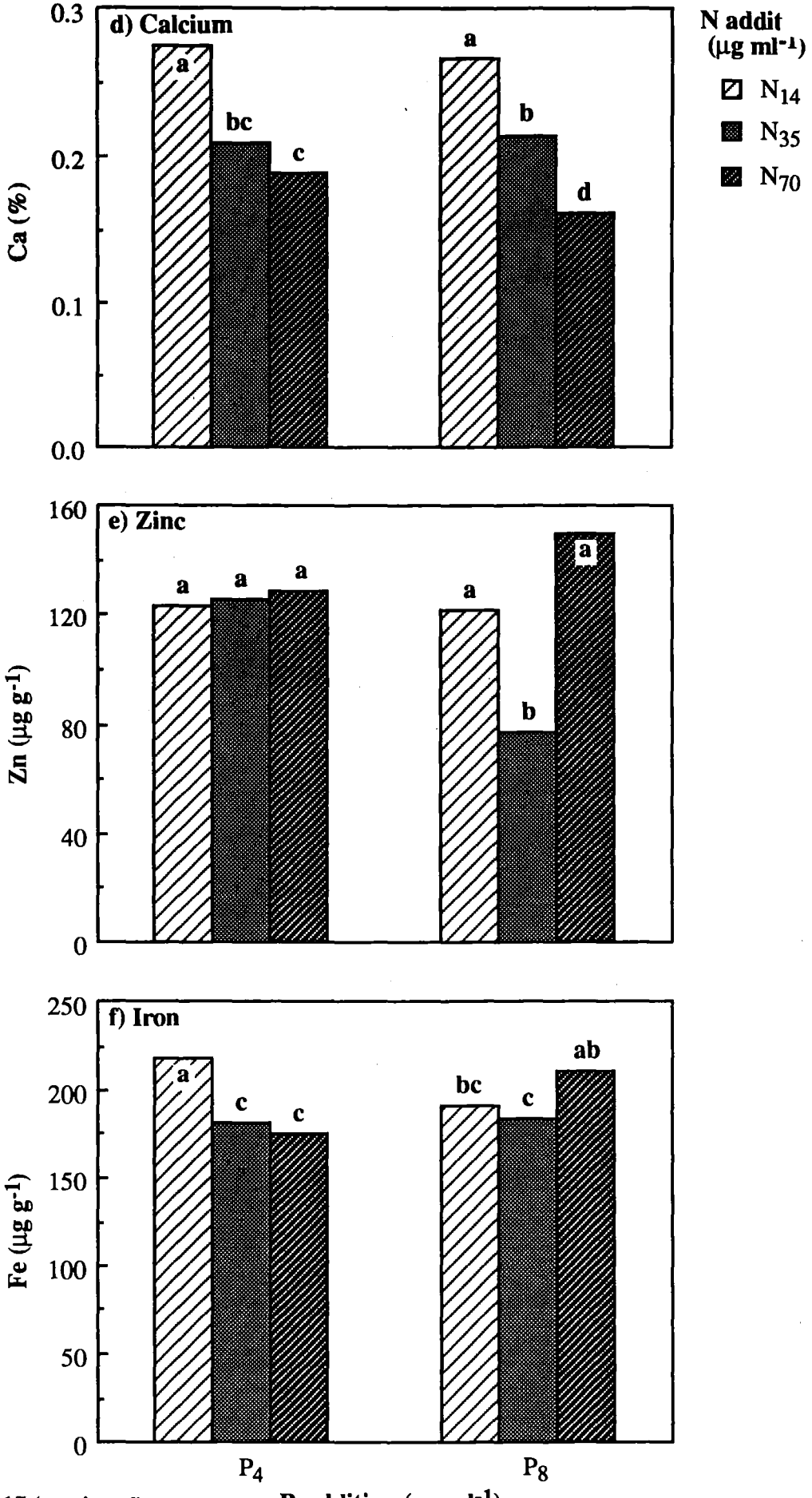

Figure 8.17 (continued)

8.3.3.3 Nutrient:N ratios at harvest 2

The rate of P addition had a significant effect on P:N ($p<.001$), Cu:N ($p<.001$), B:N ($p=.091$) and Fe:N ($p<.001$) ratios in the shoots at harvest 2. The P:N ratios were significantly ($p<.05$) higher for the P_8 rate while Cu:N and Fe:N ratios were significantly higher for the P_4 rate (**Table 8.22**).

There was a significant ($p=.081$) interaction between P and N addition on P:N ratios in the shoots (**Figure 8.18**). Within both rates of P, increasing N addition resulted in a significant ($p<.05$) decrease in P:N ratios from N_{14} to N_{35}. In the P_8 pot trial the P:N ratio also significantly ($p<.05$) decreased from N_{35} to N_{70}. For all rates of N, P:N ratios were significantly ($p<.05$) higher for P_8.

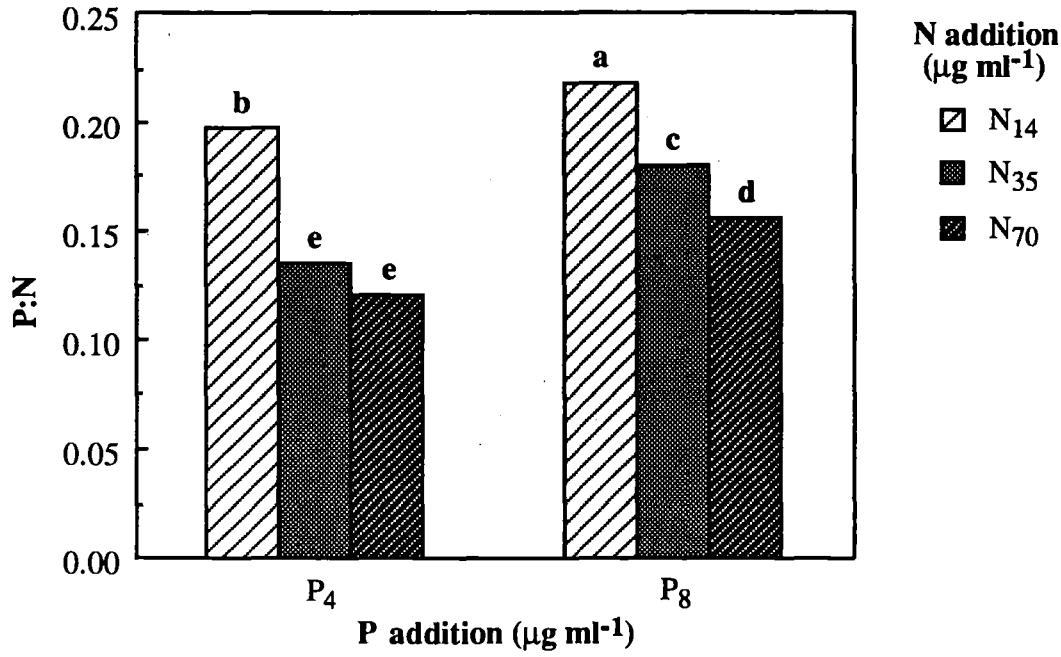

Figure 8.18: Significant interactions between P and N addition on P:N ratios in the shoots of radiata pine seedlings at harvest 2 of the P_4 and P_8 sand culture pot trials. Means with the same letter were not significantly different ($p<.05$).

In the roots at harvest 2, P addition had a significant effect on P:N ($p<.001$) and Ca:N ($p=.024$) ratios. The P:N ratios were significantly ($p<.05$) higher for P_8 while Ca:N ratios were significantly higher for P_4 (**Table 8.22**).

In the roots there was a significant interaction between P and N addition on P:N ($p<.001$), Cu:N ($p=.047$) and Fe:N ($p=.006$) ratios at harvest 2. In both P rates, P:N ratios significantly ($p<.05$) decreased with increasing N addition (**Figure 8.19a**). At each rate of N, the P:N ratios were significantly lower in the P_8 pot trial.

In the roots, the Cu:N ratios significantly decreased with increasing N addition for both P rates (**Figure 8.19b**). In the P_4 pot trial the greatest decrease occurred as N addition increased from 35 to 70µg ml^{-1} while in the P_8 pot it occurred as N increased from 14 to 35µg ml^{-1}.

The Fe:N ratios in the roots also decreased with increasing N addition for P_4 (**Figure 8.19c**). In the P_8 pot trial the Fe:N ratios in the roots significantly ($p<.05$) decreased from N_{14} to N_{35}.

Table 8.22: Effect of P addition on the nutrient:N ratios in the shoots and roots of radiata pine seedlings at harvest 2 of the P_4 and P_8 sand culture pot trials. For each nutrient:N ratio in the shoots or roots, means followed by the same letter were not significantly different ($p<.05$).

	P:N	K:N	Ca:N	Mg:N	Cu:N	Zn:N	B:N	Fe:N
Shoots:								
P_4	0.151 b	0.93 a	0.097 a	0.072 a	285 a	1079 a	1197 a	1531 a
P_8	0.185 a	0.89 a	0.095 a	0.069 a	228 b	1007 a	1111 a	1324 b
Roots:								
P_4	0.171 b	1.24 a	0.151 a	0.073 a	554 a	8447 a	694 a	12909 a
P_8	0.276 a	1.16 a	0.139 b	0.072 a	545 a	7486 a	685 a	12341 a

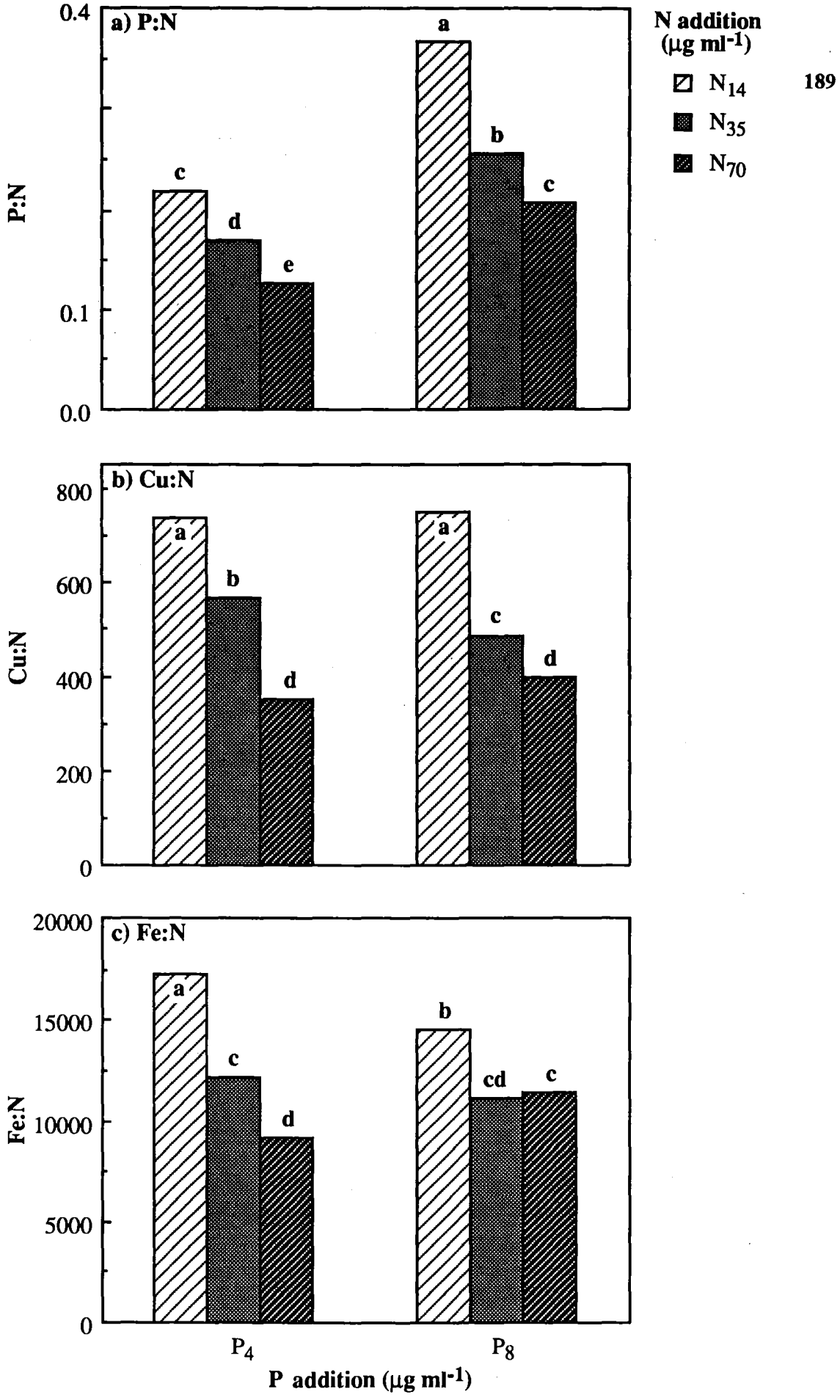

Figure 8.19: Significant interactions between P and N on nutrient:N ratios in the roots of radiata pine seedlings at harvest 2 of the P_4 and P_8 sand culture pot trials. For each nutrient:N ratio, means with the same letter were not significantly different ($p<.05$).

8.3.3.4 Amounts of nutrients

At harvest 1, the rate of P addition significantly affected the amounts of N (p=.066), P (p<.011), K (p=.082), Mg (p=.010), Cu (p=.021), Zn (p<.001) and B (p=.054) in the shoots of radiata pine seedlings. The amounts of P, Mg and Zn in the shoots pot^{-1} were significantly (p<.05) higher for the P_8 addition while the amount of Cu was higher at P_4 (**Table 8.23a**).

An interaction between P and N significantly affected the amounts of N (p=.043), Cu (p=.064) and Fe (p=.002) in the shoots. The amount of N pot^{-1} was significantly (p<.05) lower at N_{14} in both rates of P addition (**Figure 8.20a**). As N addition increased the amount of N significantly increased from N_{14} to N_{35}, for both rates of P. There was no significant difference between the amount of N in N_{35} and N_{70}, for both P rates, but the amount of N for N_{70} at P_8 (56.9mg pot^{-1}) was significantly (p<.05) higher than for N_{70} at P_4 (47.4mg pot^{-1}).

The amount of Cu pot^{-1} was significantly (p<.05) higher at N_{35} for the P_4 rate than all the other P and N combinations (**Figure 8.20b**).

In the P_4 rate there was no significant (p<.05) difference between the amount of Fe pot^{-1} for each N addition (**Figure 8.20c**). However, as N addition increased within the P_8 pot trial, the amount of Fe pot^{-1} significantly (p<.05) increased.

At harvest 1, the rate of P addition also significantly affected the amounts of P (p<.001), Cu (p<.001), Zn (p=.003) and Fe (p=.043) in the roots which were significantly (p<.05) greater for the P_8 rate (**Table 8.23a**).

At harvest 2, the rate of P significantly affected the amounts of N (p=.001), P (p<.001), Ca (p=.064), Mg (p=.040) and Cu (p=.003) in the shoots pot^{-1}. The amount of N, P and Mg was significantly higher for P_8 while Cu was significantly higher for P_4 addition (**Table 8.23b**).

The interaction between P and N was significant in affecting the shoot amount of P (p<.001) and Ca (p=.067). Within the P_8 pot trial, increasing N addition significantly (p<.05) increased the amount of P in the shoots (**Figure 8.21a**). In the P_4 pot trial, increasing N addition from 14 to 35μg ml^{-1} significantly increased the amount of P. At each rate of N, the amount of P was significantly (p<.05) higher in the P_8 pot trial.

The amount of Ca was significantly (p<.05) lower for the N_{14} addition in the P_4 pot trial than for any of the other P and N combinations (**Figure 8.21b**).

The interaction between P and B addition significantly affected the amount of K (p=.099) and Ca (p=.041) in the seedling shoots at harvest 2. Within each rate of P addition the effect of increasing B addition was not significant (p<.05) for the amount of K in the shoots (**Figure 8.22a**). The amount of K at B_1 was significantly lower with the P_4 rate than the P_8 rate. The amount of Ca in the shoots significantly (p<.05) decreased as B addition increased in the P_4 pot trial from 0.05 to 0.1μg ml^{-1} (**Figure 8.22b**). There was no significant difference between the rates of B addition on the shoot amount of Ca in the P_8 pot trial.

In the roots at harvest 2, the rate of P was significant in affecting the amounts of P (p<.001), K (p=.086), Ca (p=.007) and Zn (p=.078) pot^{-1}. The amounts of P were significantly (p<.05) higher for the P_8 rate (**Table 8.23b**) while the amount of Ca was significantly (p<.05) higher for P_4.

Table 8.23: Effect of P addition on the amount of nutrients in the shoots and roots of radiata pine seedlings per pot at two harvests of the P_4 and P_8 sand culture pot trials. For each nutrient in the shoots or roots at each harvest, means followed by the same letter were not significantly different ($p<.05$).

a) Harvest 1	N	P	K	Ca	Mg	Cu	Zn	B	Fe
Shoots:	--- mg pot^{-1} ---					--- µg pot^{-1} ---			
P_4	46 a	6.1 b	33 a	3.0 a	2.6 b	15.0 a	68 b	42 a	67 a
P_8	49 a	7.3 a	37 a	3.2 a	2.9 a	13.3 b	79 a	46 a	67 a
Roots:									
P_4	9.5 a	1.72 b	10.1 a	1.08 a	0.56 a	5.0 b	73 b	5.0 a	110 b
P_8	10.0 a	2.29 a	9.6 a	1.01 a	0.52 a	7.2 a	91 a	5.0 a	125 a

b) Harvest 2	N	P	K	Ca	Mg	Cu	Zn	B	Fe
Shoots:	--- mg pot^{-1} ---					--- µg pot^{-1} ---			
P_4	137 b	19.4 b	122 a	12.4 a	9.4 b	38 a	142 a	154 a	206 a
P_8	153 a	27.1 a	129 a	13.3 a	10.0 a	34 b	144 a	159 a	200 a
Roots:									
P4	33 a	5.6 b	40 a	4.9 a	2.4 a	17.9 a	277 a	23 a	417 a
P8	33 a	8.7 a	36 a	4.4 b	2.3 a	17.2 a	231 a	22 a	392 a

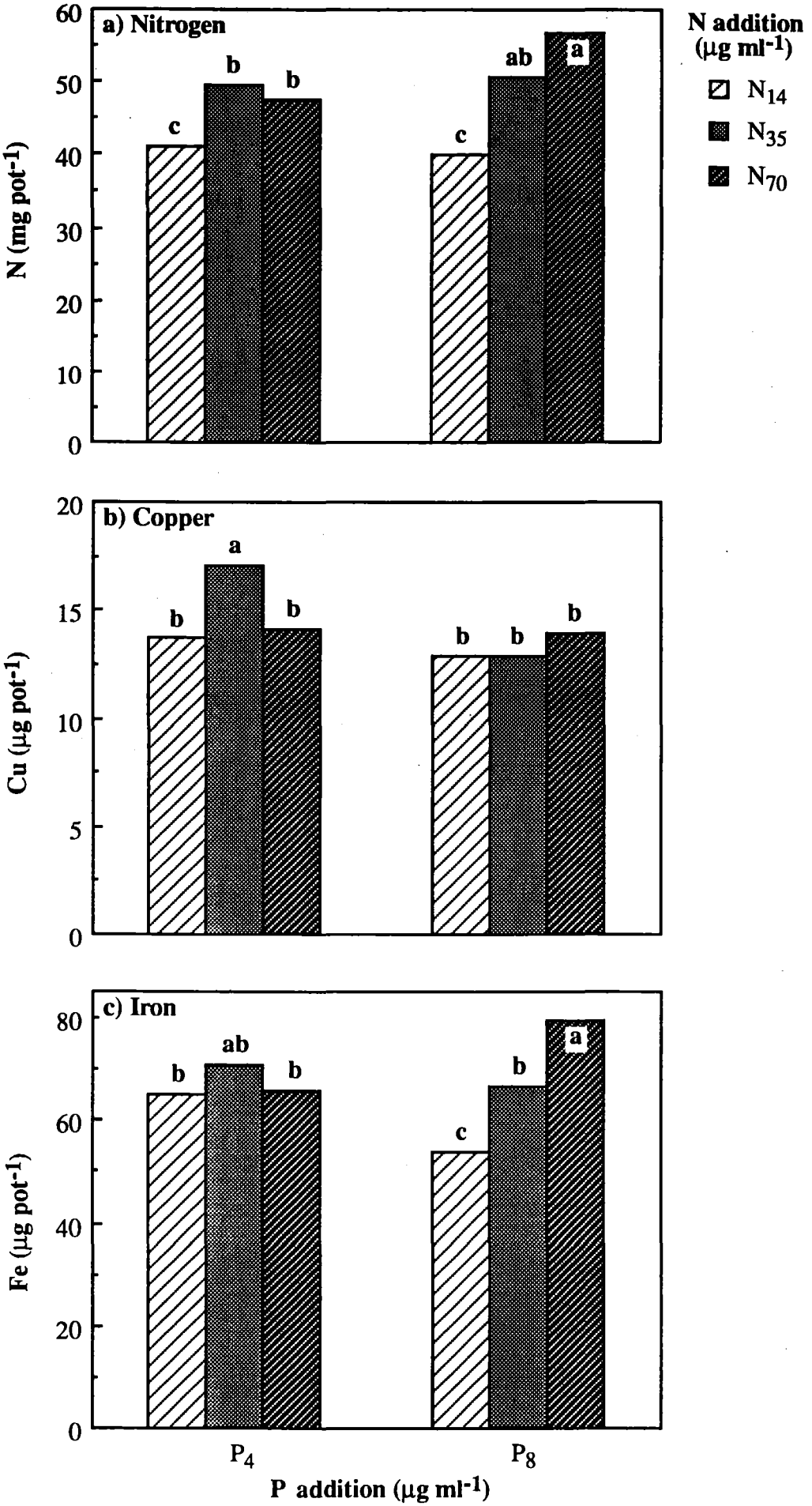

Figure 8.20: Significant interactions between P and N addition on the amount of nutrients in the shoots of radiata pine seedlings per pot at harvest 1 of the P_4 and P_8 sand culture pot trials. For each nutrient, means with the same letter were not significantly different ($p<.05$).

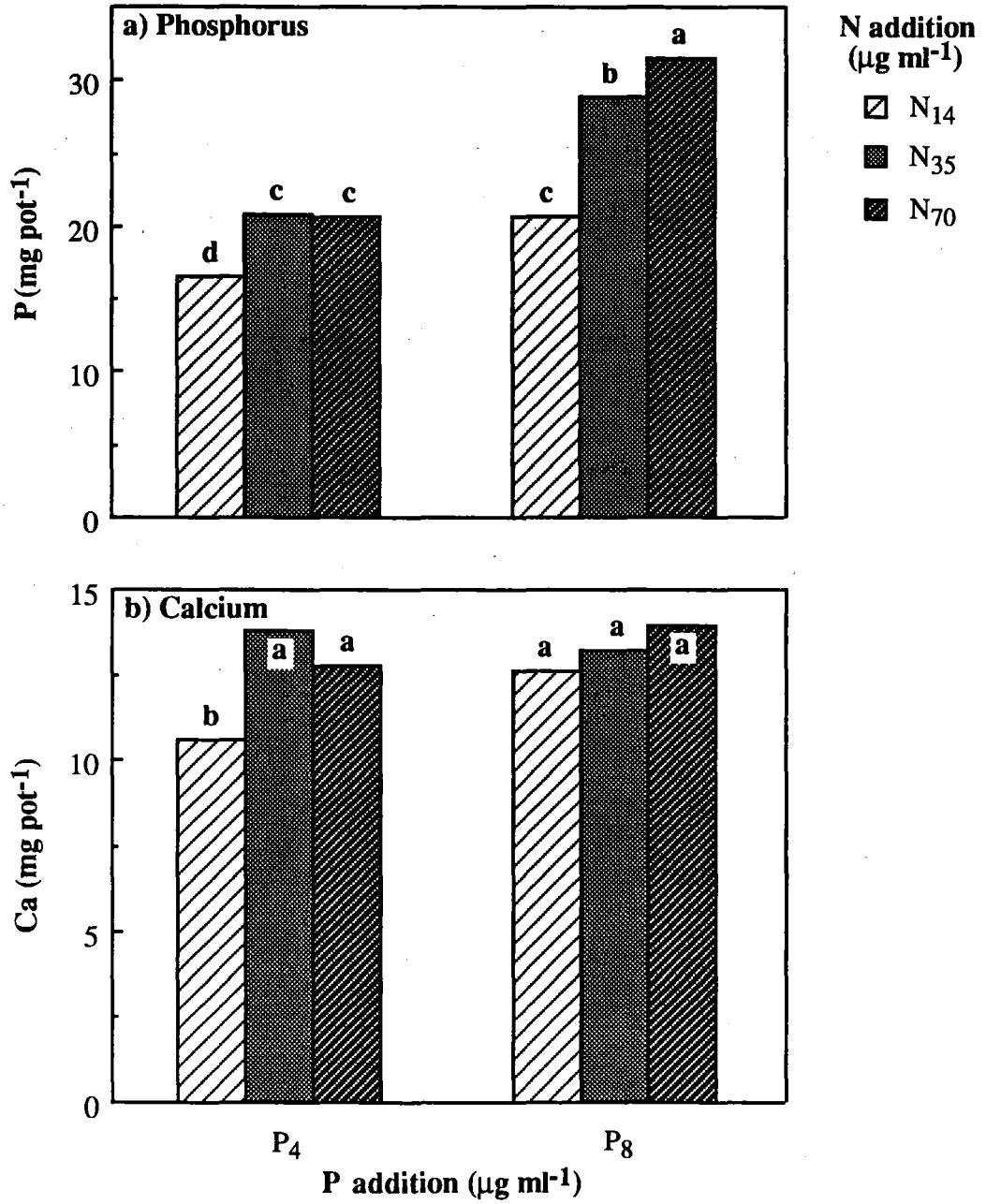

Figure 8.21: Significant interactions between P and N addition on the amount of nutrients in the shoots of radiata pine seedlings per pot at harvest 2 of the P_4 and P_8 sand culture pot trials. For each nutrient, means with the same letter were not significantly different ($p<.05$).

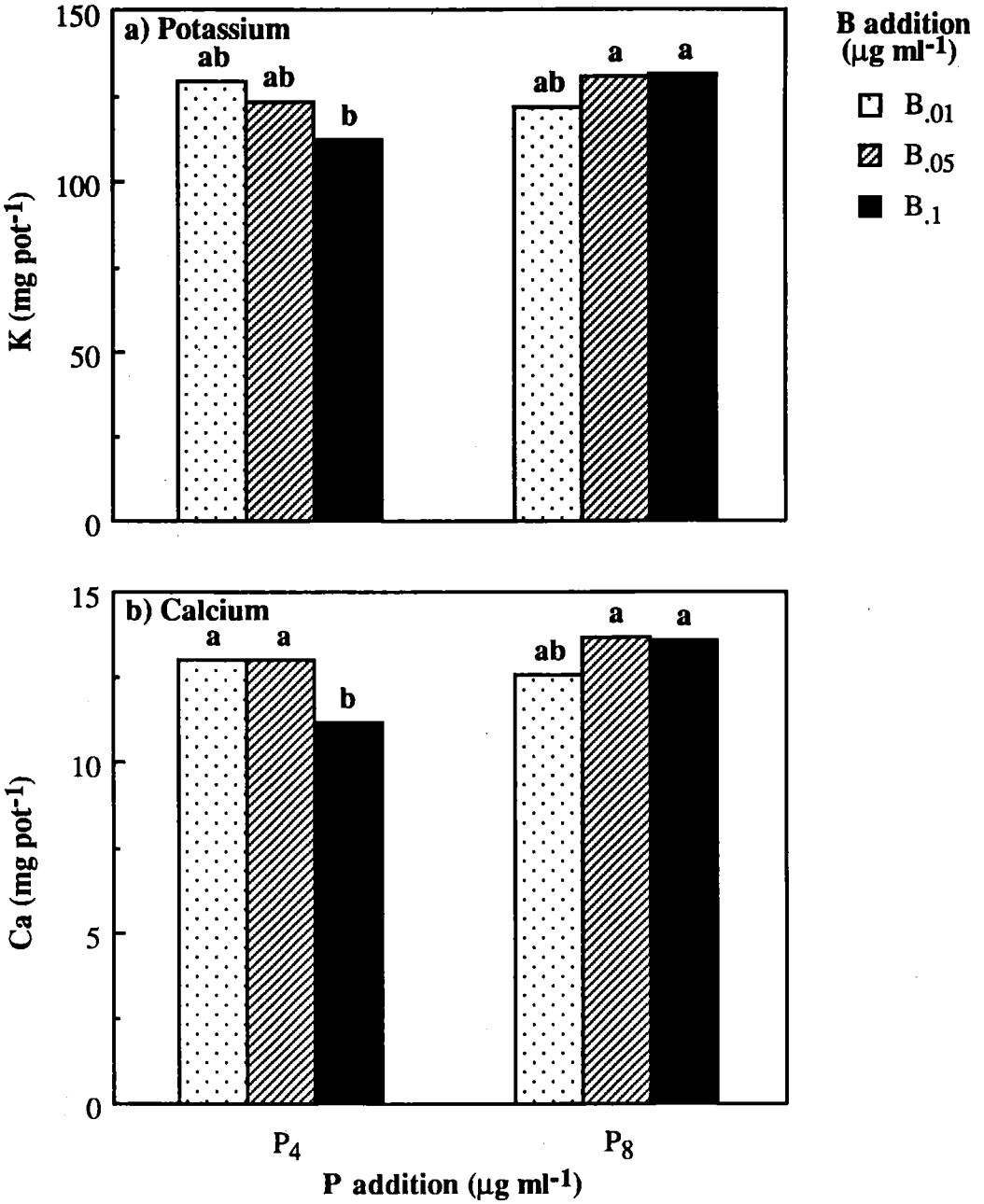

Figure 8.22: Significant interactions between P and B addition on the amount of nutrients in the shoots of radiata pine seedlings per pot at harvest 2 of the P_4 and P_8 sand culture pot trials. For each nutrient, means with the same letter were not significantly different ($p<.05$).

The interaction between P and N addition significantly affected the amounts of P ($p=.057$) and Fe in the roots ($p=.012$). Within both rates of P, increasing N addition from 14 to 35µg ml^{-1} resulted in significant decreases in the amount of P in the roots (**Figure 8.23a**). For each rate of N, the amount of P pot^{-1} in the roots was significantly higher in the P_8 pot trial.

The amount of Fe pot^{-1} in the roots significantly ($p<.05$) declined at both rates of P when N addition increased from 14 to 35µg ml^{-1} (**Figure 8.23b**). At N_{14}, the amount of Fe pot^{-1} was significantly higher for the P_4 than for the P_8 rate.

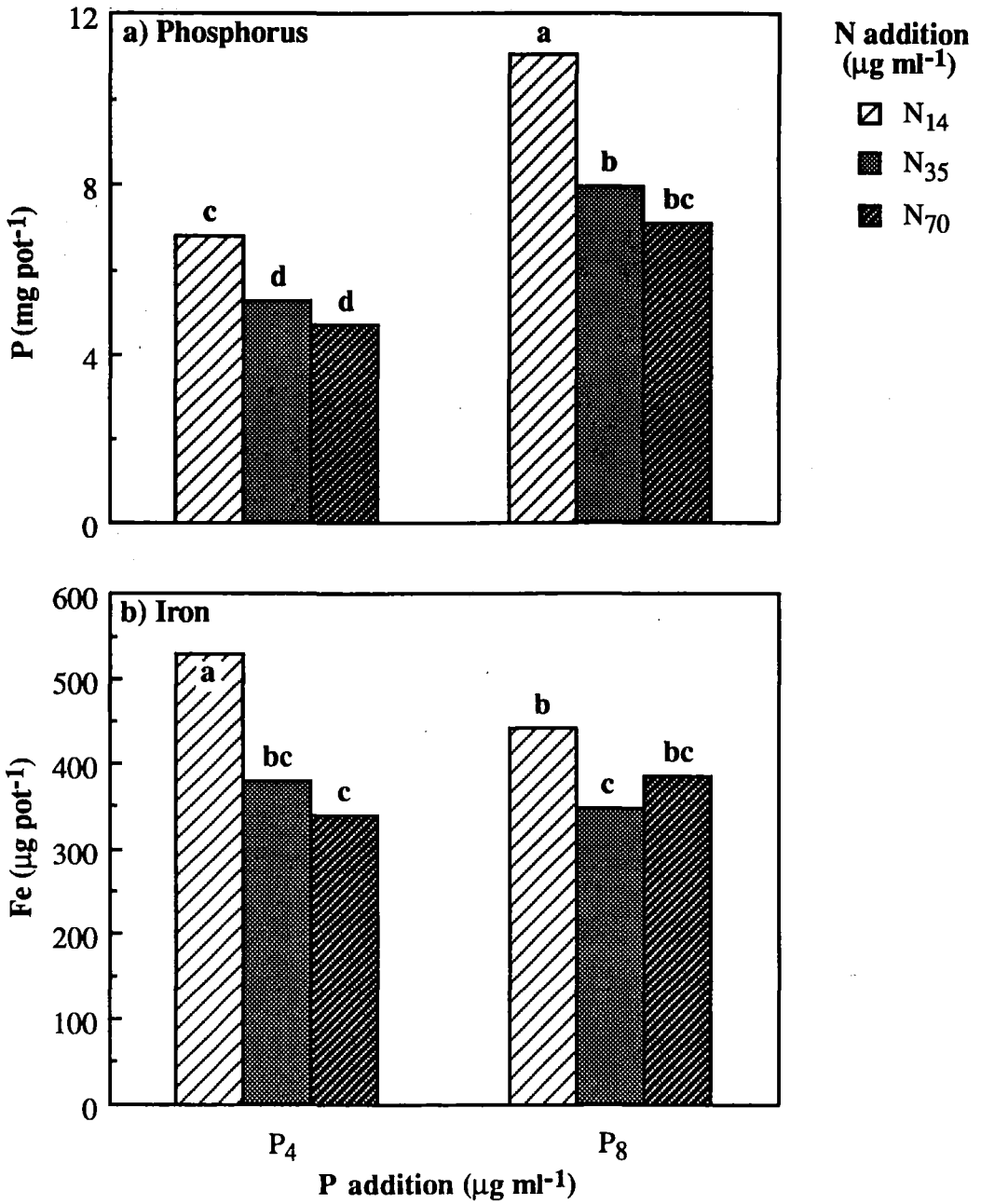

Figure 8.23: Significant interactions between P and N addition on the amount of nutrients in the roots of radiata pine seedlings per pot at harvest 2 of the P_4 and P_8 sand culture pot trials. For each nutrient, means with the same letter were not significantly different ($p<.05$).

The interaction between P and B addition significantly affected the amounts of Zn ($p=.052$) in the roots. The addition of $B_{.05}$ in the P_8 pot trial resulted in a significant ($p<.05$) decrease in the amount of Zn in the roots compared to all the other P and B combinations (**Figure 8.24**).

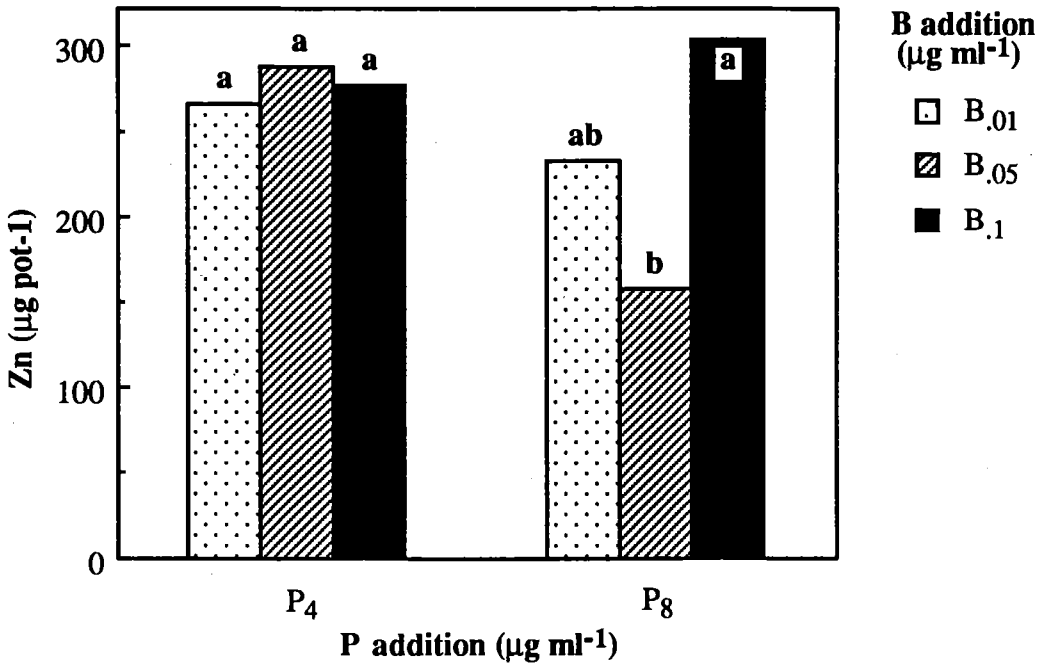

Figure 8.24: Significant interactions between P and B addition on the amount of Zn in the roots of radiata pine seedlings per pot at harvest 2 of the P_4 and P_8 sand culture pot trials. Means with the same letter were not significantly different ($p<.05$).

8.3.3.5 Total amount of nutrients per pot at harvest 2

The rate of P addition had a significant effect on the total amount of N ($p=.005$), P ($p<.001$), Cu ($p=.004$) and Zn ($p=.089$) pot^{-1}. The total amounts of N and P pot^{-1} were significantly ($p<.05$) higher with the P_8 rate of addition **(Table 8.24)** while the total amount of Cu was significantly higher for the P_4 rate.

The interaction between P and N addition was significant for the total amounts of P ($p=.015$) and Fe ($p=.018$) pot^{-1}. Within each rate of P addition, increasing N from 14 to 35µg ml^{-1} significantly ($p<.05$) increased the total amount of P pot^{-1} in the seedlings **(Figure 8.25a)**. For all rates of N, the total amount of P was higher in the P_8 pot trial.

In the P_4 pot trial, the total amount of Fe pot^{-1} significantly ($p<.05$) decreased from N_{14} to N_{70} while for P_8 the amount of Fe significantly increased from N_{35} to N_{70} **(Figure 8.25b)**.

There was a significant P and B interaction for the total amounts of K ($p=.073$), Ca ($p=.018$) and Zn ($p=.036$) pot^{-1}. In the P_4 pot trial, there was a significant ($p<.05$) decrease in the total amount of K **(Figure 8.26a)** and Ca **(Figure 8.26b)** in the seedlings as N addition increased from N_{14} to N_{70}. There were no significant differences between the rates of B on the total amount of K and Ca in the P_8 pot trial.

Table 8.24: Effect of P addition on the total amount of nutrients in the radiata pine seedlings per pot at harvest 2 of the P_4 and P_8 sand culture pot trials. For each nutrient, means followed by the same letter were not significantly different ($p<.05$).

	N	P	K	Ca	Mg	Cu	Zn	B	Fe
	--- mg pot^{-1} ---					--- µg pot^{-1} ---			
P_4	171 b	25 b	162 a	17.3 a	11.8 a	56 a	419 a	177 a	623 a
P_8	185 a	36 a	165 a	17.7 a	12.2 a	51 b	375 a	181 a	592 a

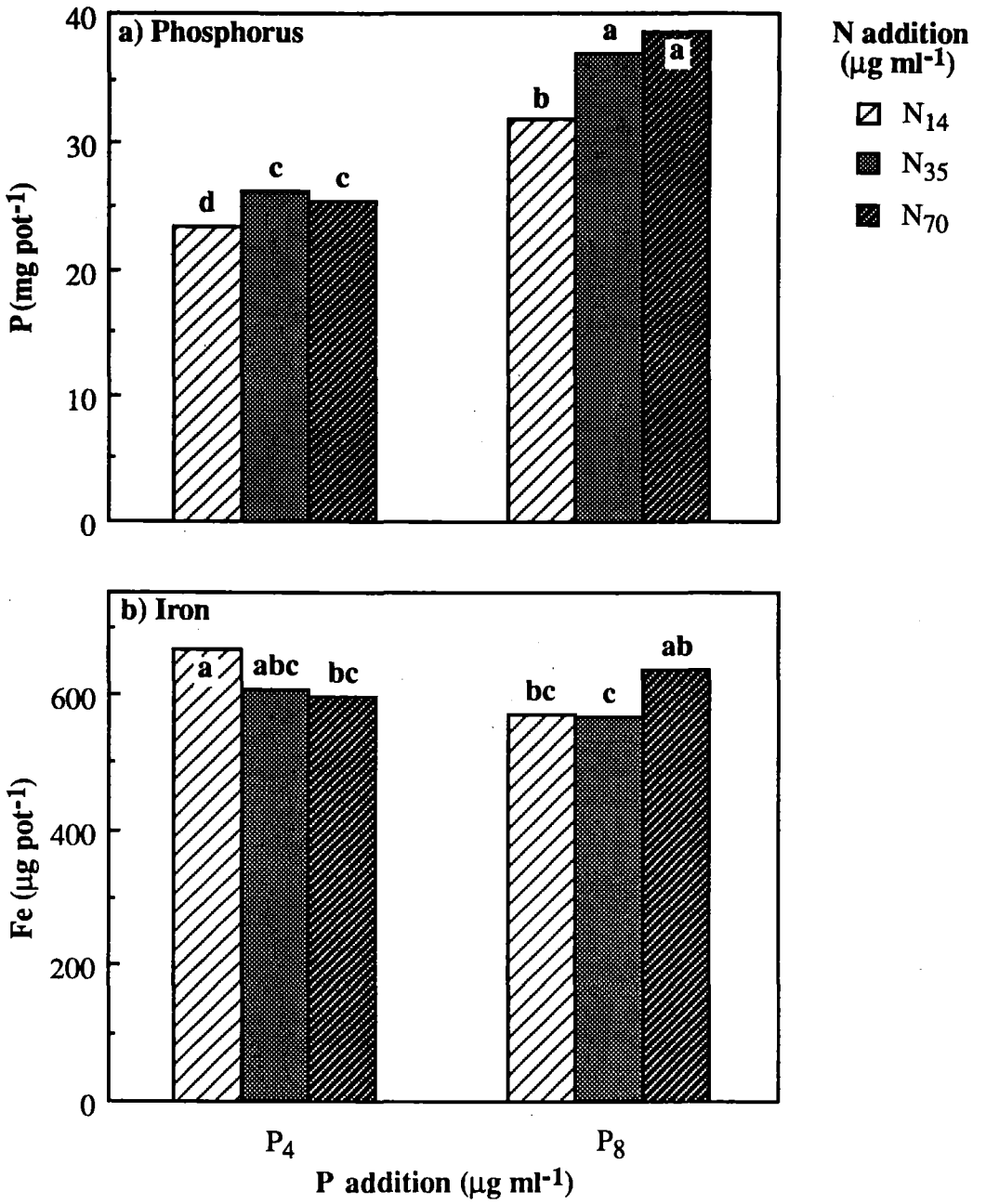

Figure 8.25: Significant interactions between P and N addition on the total amount nutrients in radiata pine seedlings per pot at harvest 2 of the P_4 and P_8 sand culture pot trials. For each nutrient, means with the same letter were not significantly different ($p<.05$).

The total amount of Zn was significantly ($p<.05$) lower for $B_{.05}$ in the P_8 pot trial compared to the other combinations of P and B in both pot trials (**Figure 8.26c**).

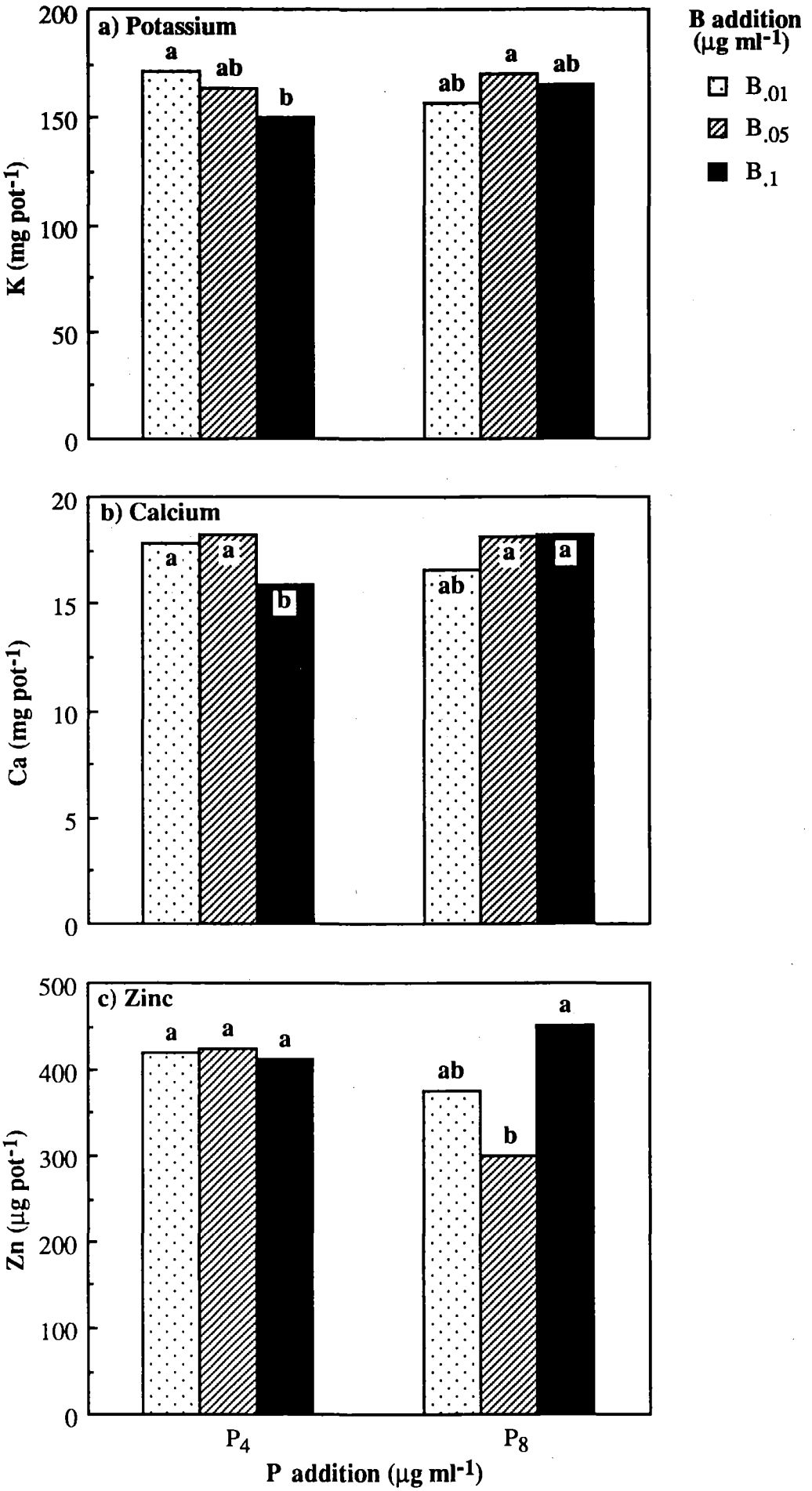

Figure 8.26: Significant interactions between P and B addition on the total amount nutrients in radiata pine seedlings per pot at harvest 2 of the P_4 and P_8 sand culture pot trials. For each nutrient, means with the same letter were not significantly different ($p<.05$).

8.3.3.6 Efficiency of nutrient uptake by the roots at harvest 2

The efficiency of root uptake of N, P, K, Ca, Mg and B was significantly affected by the rate of P addition (**Table 8.25**) and their efficiency of uptake was significantly ($p<.05$) higher in the P_8 pot trial.

The root efficiency of Fe uptake was significantly ($p=.008$) affected by an interaction between added P and N (**Figure 8.27**). Within the P_8 pot trial, increasing N addition significantly ($p<.05$) increased the root efficiency of Fe uptake. In the P_4 pot trial the root efficiency of Fe uptake significantly increased as N addition increased from 14 to 70μg ml^{-1}.

An interaction between P and B addition significantly ($p=.087$) affected the root efficiency of Zn uptake (**Figure 8.28**). In the P_8 pot trial, B addition at 0.05μg ml^{-1} resulted in a significant ($p<.05$) decrease in the efficiency of Zn uptake. The rates of B in the P_4 pot trial had no significant effect on the efficiency of Zn uptake.

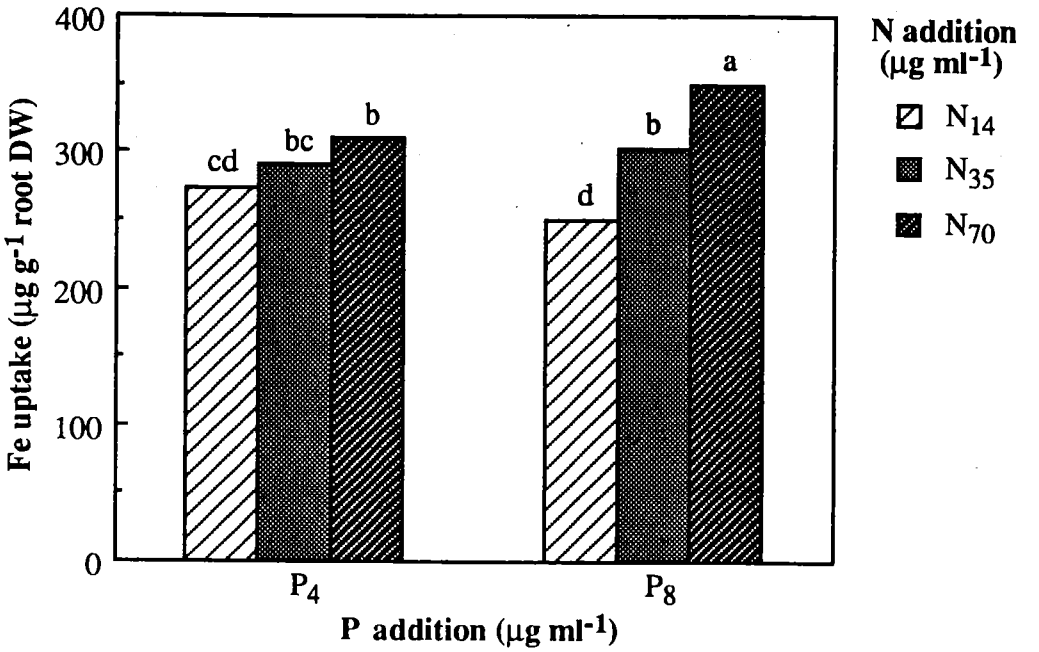

Figure 8.27: Significant interaction between P and N addition on the efficiency of Fe uptake by radiata pine seedling roots at harvest 2 of the P_4 and P_8 sand culture pot trials. Means with the same letter were not significantly different ($p<.05$).

8.3.3.7 The percentage of total nutrients in the shoots at harvest 2

The % of total seedling dry weight represented by the shoot was significantly ($p<.05$) higher in the P_8 pot trial (**Table 8.26**).

The rate of P addition across the two pot trials had a significant effect on the % of measured macronutrients found in the radiata pine seedlings. The % of total N, K, Ca and Mg was significantly ($p<.05$) higher in the P_8 shoots while the % of P was higher in the P_4 shoots.

Table 8.25: Effect of P addition and the probability of a significant P main effect (Prob. of P, NS = not significant) on the efficiency of nutrient uptake by radiata pine seedling roots at harvest 2 of the P_4 and P_8 sand culture pot trials. For each nutrient, means followed by the same letter were not significantly different ($p<.05$).

	N	P	K	Ca	Mg	Cu	Zn	B	Fe
	--- mg pot^{-1} ---					--- µg pot^{-1} ---			
P_4	82 b	11.8 b	77 b	8.1 b	5.6 b	26 a	195 a	84 b	292 a
P_8	96 a	18.4 a	84 a	8.9 a	6.3 a	26 a	191 a	93 a	301 a
Prob. of P	<.001	<.001	.037	.014	.004	NS	NS	.026	NS
CV%	13.1	17.0	15.6	13.2	13.9	13.2	23.6	14.9	9.3

Table 8.26: Effect of P addition and the probability of a significant P main effect (Prob. of P, NS = not significant) on the % of nutrients and dry weight in the shoots of radiata pine seedling at harvest 2 of the P_4 and P_8 sand culture pot trials. For each nutrient, means followed by the same letter were not significantly different ($p<.05$).

	N	P	K	Ca	Mg	Cu	Zn	B	Fe	Shoot DW
	--- % of seedling total located in the shoot ---									
P_4	79 b	77 a	75 b	72 b	79 b	67 a	36 a	87 a	34 a	77 b
P_8	82 a	75 b	78 a	76 a	81 a	66 a	42 a	88 a	34 a	78 a
Prob. of P	.005	.021	.012	<.001	.006	NS	.060	.067	NS	.002
CV%	3.5	4.6	5.4	4.7	2.8	7.5	25.0	2.2	12.2	2.4

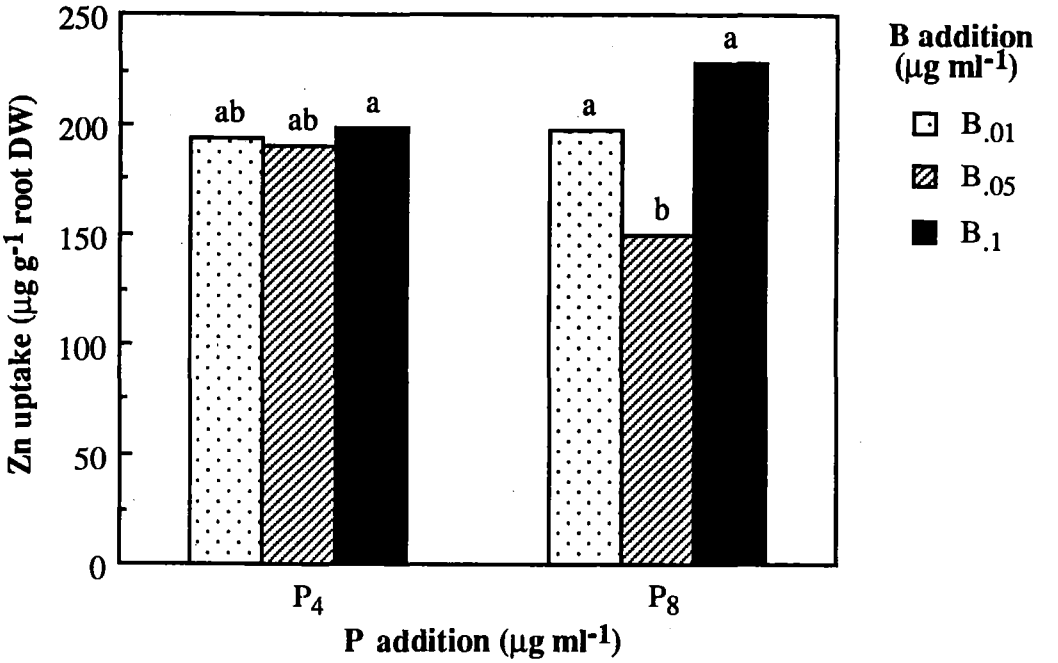

Figure 8.28: Significant interaction between P and B addition on the efficiency of Zn uptake by radiata pine seedling roots at harvest 2 of the P_4 and P_8 sand culture pot trials. Means with the same letter were not significantly different ($p<.05$).

There was a significant interaction between P and N addition on the % of P ($p=.038$), Ca ($p=.046$) and Fe ($p=.055$) found in the shoots. There was a significant increase in the % of P in the shoots (**Figure 8.29a**) as N addition in both pot trials increased from 14 to 35µg ml^{-1}. At N_{14} the % of P in the P_8 pot trial was significantly lower than that for P_4. For the % of Ca in the shoots (**Figure 8.29b**), there was a increase with increasing N addition in the P_8 pot trial while for P_4, the % of Ca increased as N addition increased from 14 to 35µg ml^{-1}. The % of Fe found in the shoots significantly increased with increasing N rate in the P_4 pot trial (**Figure 8.29c**). In the P_8 pot trial the % of Fe increased from N_{14} to N_{35}.

There was a significant ($p=.053$) interaction between P and B addition on the % of Zn in the shoots. The % of Zn in the $P_8B_{.05}$ combination, at 49.5, was significantly ($p<.05$) higher than all of the other P and B combinations which ranged from 34.8 to 40.1% of Zn in the shoots.

8.3.3.8 Physiological efficiency of nutrient use at harvest 2

The addition of P was significant for the physiological efficiency in the use of N, P, Mg, Cu and Fe (**Table 8.27**). The physiological efficiency in the use of N and P was significantly ($p<.05$) higher in the P_4 pot trial while for Cu it was significantly higher in the P_8 pot trial.

The physiological efficiency in the use of P was significantly ($p=.003$) affected by an interaction between P and N addition (**Figure 8.30**). In the P_4 pot trial the increasing addition of N significantly ($p<.05$) increased the physiological efficiency in the use of P. There was no such significant difference as a result of increasing N addition in the P_8 pot trial.

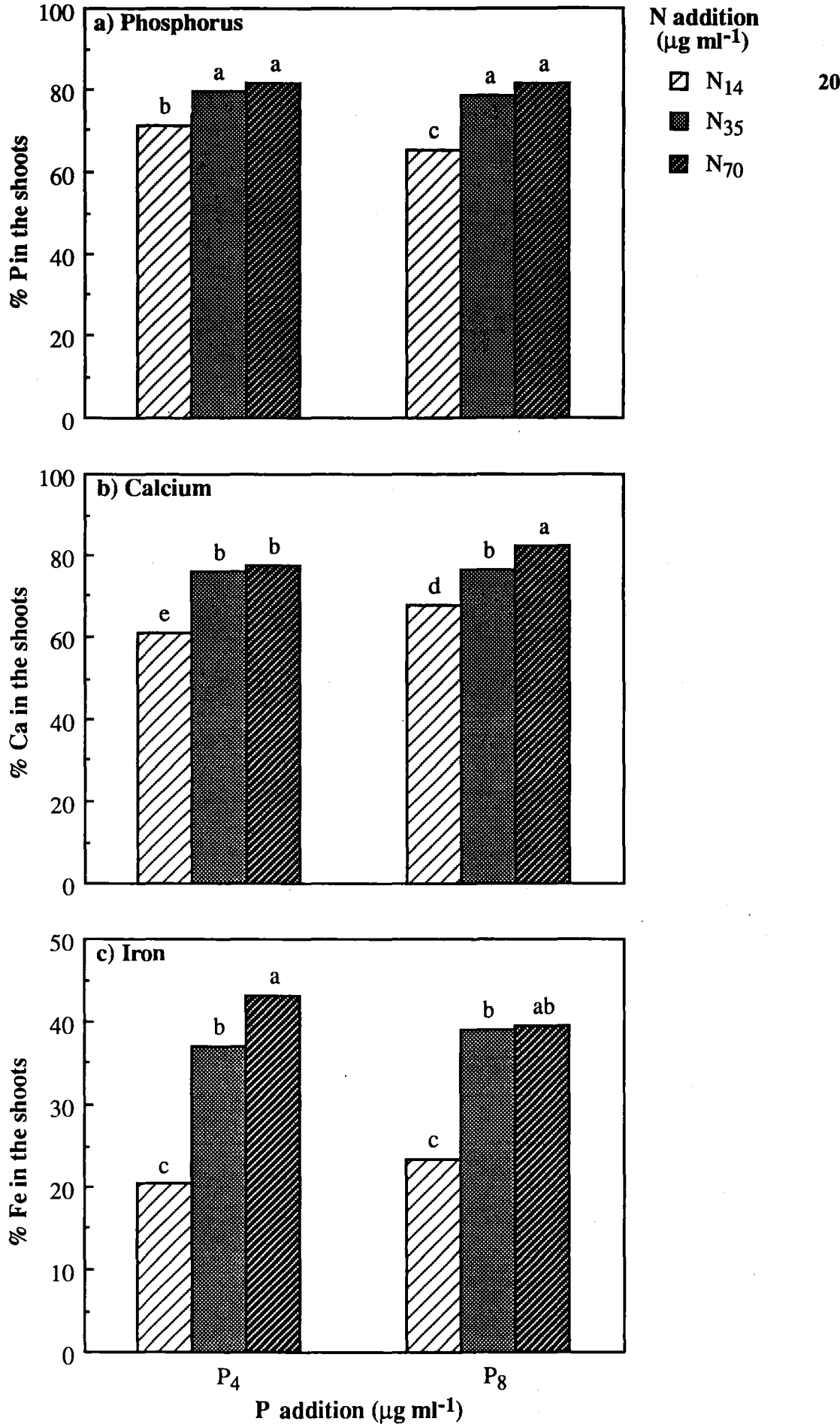

Figure 8.29: Significant interactions between P and N addition on the % of total nutrient, in radiata pine seedlings, located in the shoots at harvest 2 of the P_4 and P_8 sand culture pot trials. For each nutrient, means with the same letter were not significantly different ($p<.05$).

Table 8.27: Effect of P addition and the probability of a significant P main effect (Prob. of P, NS = not significant) on the physiological efficiency of nutrient uptake by radiata pine roots at harvest 2 of the P_4 and P_8 sand culture pot trials. For each nutrient values followed by the same letter were not significantly different ($p<.05$).

	N	P	K	Ca	Mg	Cu	Zn	B	Fe
	--- mg g^{-1} shoot dry weight ---					--- µg g^{-1} shoot dry weight ---			
P_4	56 a	378 a	61 a	593 a	781 a	196 b	53 a	48 a	37 a
P_8	51 b	277 b	59 a	563 a	748 a	226 a	50 a	47 a	39 a
Prob. of P	.007	<.001	NS	NS	.064	<.001	NS	NS	.085
CV%	11.4	11.7	15.2	13.0	8.3	12.8	14.5	10.4	11.2

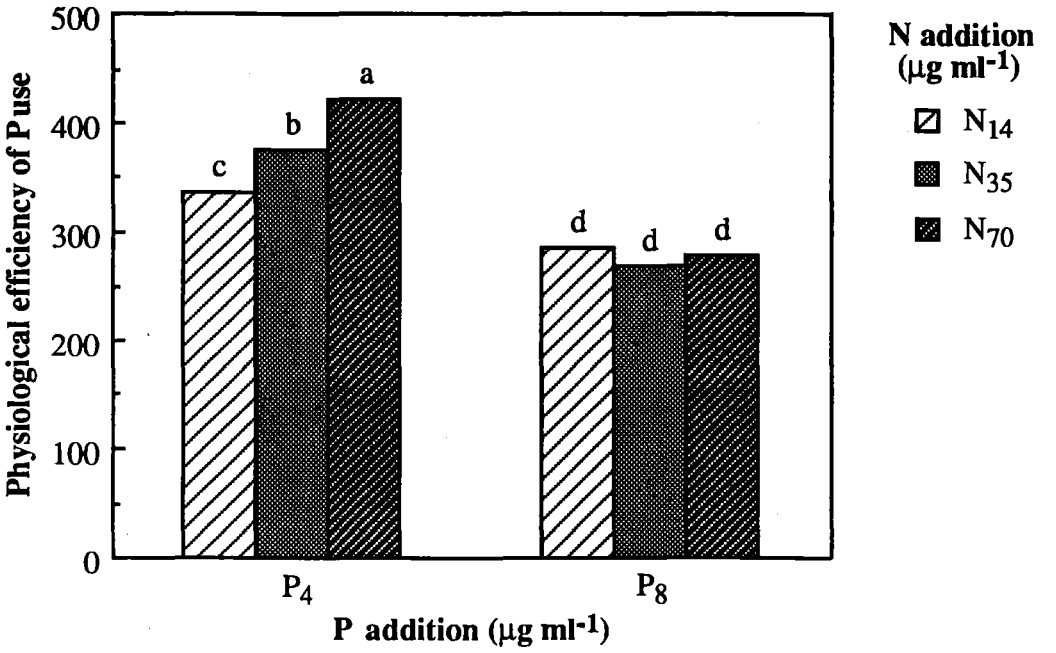

Figure 8.30: Significant interaction between P and N addition on the physiological efficiency of P use by radiata pine seedlings at harvest 2 of the P_4 and P_8 sand culture pot trials. Means with the same letter were not significantly different ($p<.05$).

8.4 DISCUSSION

8.4.1 Comparison of harvest 1 and 2 results

By harvest 2 in both pot trials, the significant effect of N, particularly on the physical growth of the seedlings, was more pronounced and significant than it had been at harvest 1. There were few significant effects on seedling physical growth at harvest 1 although B addition significantly affected the number of branches per seedling at harvest 1 of the P_8 pot trial. This did not occur at harvest 2 possibly because N addition became more significant in its promotion of general seedling growth. Also, the P rate, across the 2 pot trials, had a significant effect on shoot dry weight pot^{-1} at harvest 1 (**Table 8.20**) but this was no longer observed by harvest 2 although the shoot dry weights were still higher in the P_8 pot trial.

The effect of increasing N and B on nutrient concentrations was more obvious and significant by harvest 2 in the P_4 and P_8 pot trials. The effect of time, in allowing the different treatment effects to develop, suggested that the further calculation of various nutrient parameters could concentrate on the harvest 2 data (as indicated in the materials and methods). Given the results in the P_4 and P_8 pot trials it seems that the harvest 1 data did not generally yield additional information to that found at harvest 2. With this type of pot trial, a harvest at 2 months from the beginning of treatment addition, as occurred for harvest 1, did not appear to be necessary when a harvest was also being carried out at 4 months.

The following discussion will focus on the results from the second harvest of radiata pine seedlings from both the P_4 and P_8 pot trials.

8.4.2 Seedling growth and nutrition

8.4.2.1 The effect of N addition

At harvest 2 in both pot trials, the majority of the measured seedling growth parameters and nutrient concentrations were significantly affected by the rate of N addition which explained the greatest proportion of the data variation in the Anova.

In the P_4 pot trial the addition of N significantly affected the nutrient concentrations of N, P, Ca, B and Fe in the shoots at harvest 2 (**Table 8.3**) and also the shoot dry weight pot^{-1} (**Figure 8.2a**). The concentrations of N and Fe increased with increasing N addition while P, Ca and B decreased.

There was a significant and positive correlation between N concentrations and shoot dry weight in the P_4 pot trial - as shoot N concentrations increased so did the shoot dry weight pot^{-1} (**Figure 8.31**).

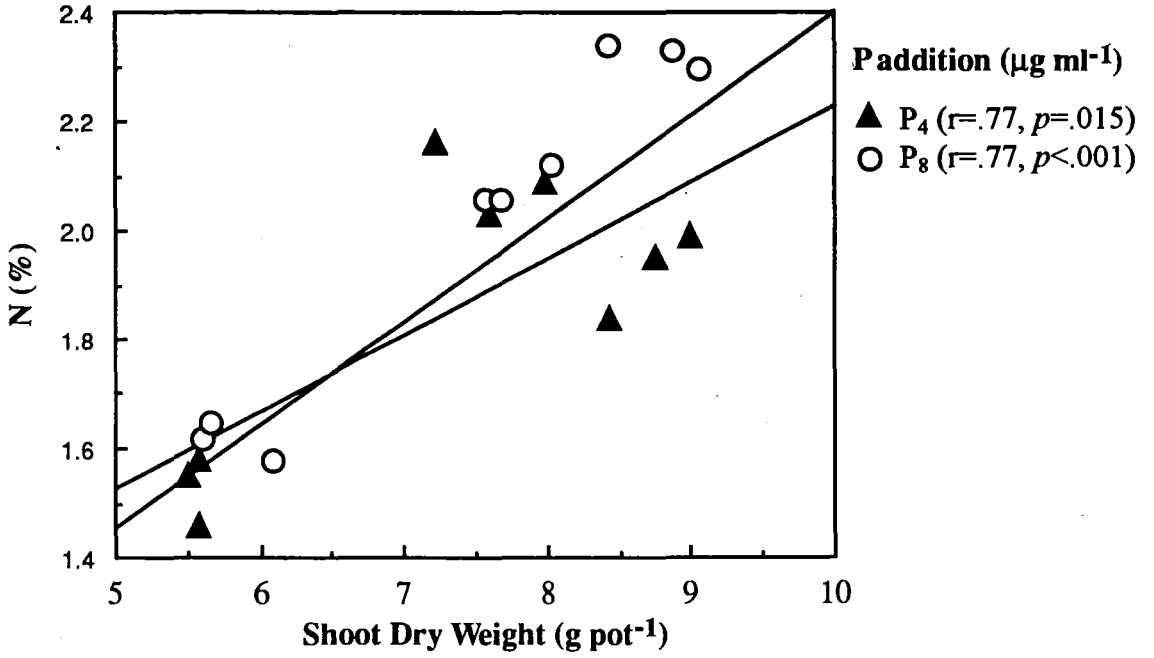

Figure 8.31: Correlation between the shoot concentrations of N and shoot dry weights per pot of radiata pine seedlings in the P_4 and P_8 sand culture pot trials at harvest 2.

The correlations between the shoot concentrations of N and Ca (r=.56, p=.12) or P (r=.54, p=.13) were negative. This decline in Ca and P concentrations with increasing N concentrations may have been a result of dilution as the N concentrations were positively correlated with increasing shoot dry weight production and further correlations indicated that as shoot dry weight increased the concentrations of P, Ca and B decreased (**Table 8.28**).

A similar trend was also observed in the P_8 pot trial. Here the addition of N significantly affected the shoot concentrations of N, Ca, B and Fe (**Table 8.12**) where N, Cu and Fe concentrations generally increased with increasing N addition, while Ca and B decreased. The shoot concentrations of N were significantly and positively correlated with shoot dry weights pot^{-1} (**Figure 8.31**). The correlations between N concentrations and Ca (r=.90, p=.018), Zn (r=.76, p=.018) and B (r=.65, p=.060) were significant and negative. With increasing shoot dry weight in the P_8 pot trial, the shoot concentrations of Ca, Zn and B declined, while the Fe concentrations increased (**Table 8.28**).

Table 8.28: Significant correlations (r) between shoot nutrient concentrations and shoot dry weight pot^{-1} of radiata pine seedlings at harvest 2 of the low P_4 and P_8 sand culture pot trials.

Nutrient	P_4: r	Probability	P_8: r	Probability
Fe ↑*	.75	.020	.92	<.001
P ↓	.85	.004	-	-
Ca ↓	.71	.033	.94	<.001
Zn ↓	-	-	.81	.008
B ↓	.61	.080	.64	.063

* The direction of the arrow indicates if nutrient concentrations increased (↑) or decreased (↓) as shoot dry weights pot^{-1} increased.

If dilution had occurred in both pot trials, the amount of nutrient uptake into the larger shoots, associated with the N_{35} and N_{70} rates, should not have been significantly less than the amounts of nutrient in the smaller N_{14} shoots. The shoot amounts of Ca, B and P in the P_4 pot trial (**Table 8.6**) and Ca, B and Zn in the P_8 pot trial (**Table 8.15**) were higher, significantly so for some treatments, for N_{35} and N_{70} compared to the N_{14} rate. It appears that the promotion of seedling shoot growth, by increasing N addition, was not matched by the uptake of nutrients such as P, Ca, B and Zn - while the amounts of these nutrients were higher in the shoots of N_{35} and N_{70}, their concentrations declined indicating that dilution had taken place.

The correlation between shoot N and Fe concentrations was positive and highly significant for both the P_4 and P_8 pot trials (**Figure 8.32**). As the shoot concentrations of N increased so did the concentrations of Fe and there was a distinct separation between the N_{14} treatments (symbols in the lower left of the graph) and the N_{35} and N_{70} treatments. In the P_4 pot trial there was not the obvious difference between the N_{35} and N_{70} rates that was observed in the P_8 pot trial. This was related to the significantly higher shoot N concentrations at N_{70}, compared to N_{35} in the P_8 pot trial (**Table 8.12**) and not to any significant difference in shoot Fe concentrations. In the P_4 pot trial there was no significant difference in the shoot N concentrations at the N_{35} and N_{70} rates (**Table 8.3**).

The addition of N, while increasing shoot production in the radiata pine seedlings had the opposite effect on root dry weight production in the two pot trials at harvest 2. The correlation between shoot and root dry weights was negative and significant, particularly in the P_8 pot trial, where higher shoot weights were associated with lower root weights pot^{-1} (**Figure 8.33**). For both pot trials, the major treatment differences were between the N_{35} and N_{70} values (lower right region of the graph) and the N_{14} values (upper left). Thus with increasing N addition shoot dry weights pot^{-1} significantly ($p<.05$) increased while root dry weights decreased (significantly in the P_4 pot trial). The resulting shoot:root ratios were therefore significantly increased by increasing N addition from 14 to 35μg ml^{-1}. This change in dry weight partitioning from the roots to the shoots with increasing N addition from 14 to 35μg ml^{-1} was also found in the ammonium versus nitrate pot trial (**Figure 7.4**) where the source of N was not significant.

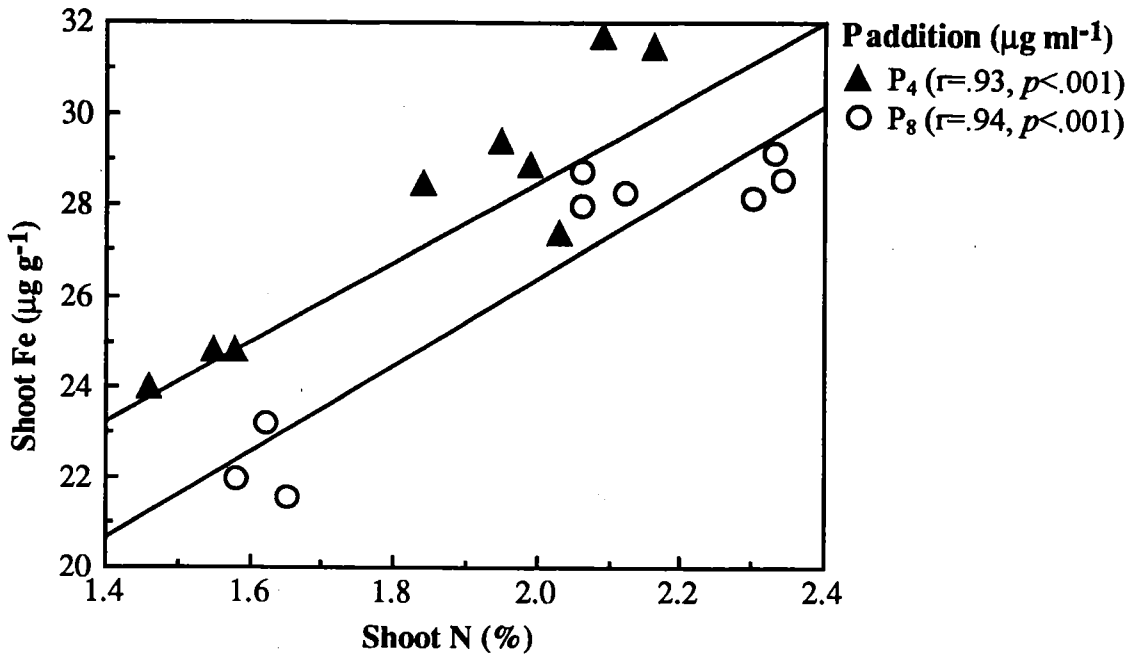

Figure 8.32: Correlation between the shoot concentrations of N and Fe of radiata pine seedlings in the P_4 and P_8 sand culture pot trials at harvest 2.

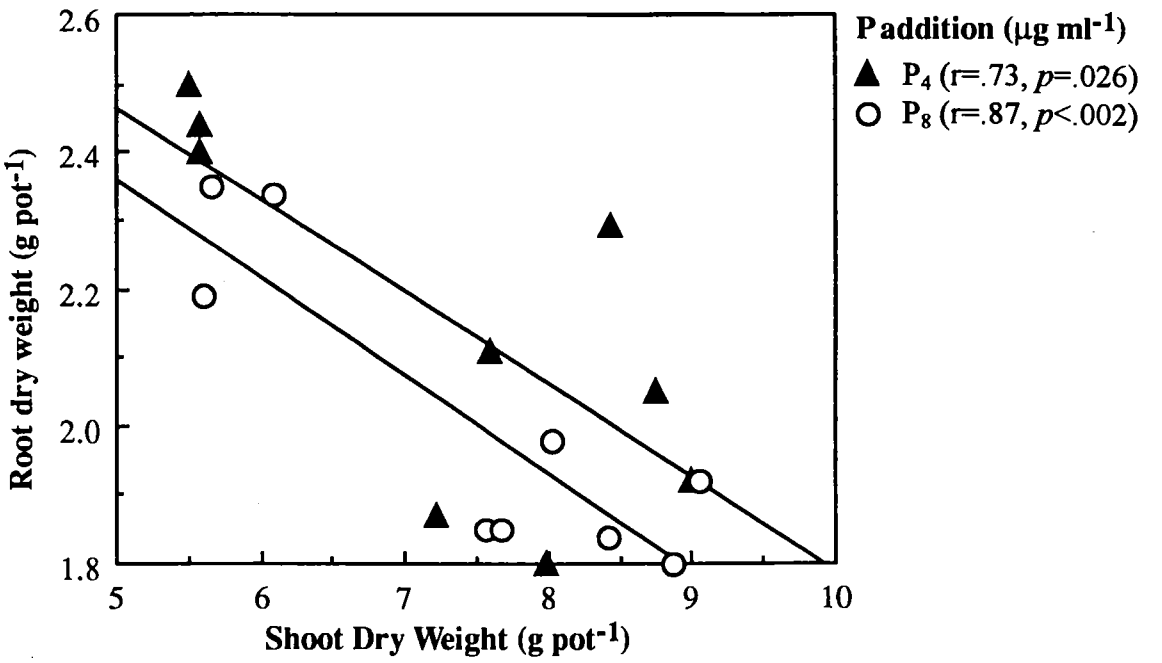

Figure 8.33: Correlation between the shoot and root dry weights of radiata pine seedlings per pot in the P_4 and P_8 sand culture pot trials at harvest 2.

With increasing N addition the root concentrations of N significantly ($p<.05$) increased in both pot trials. However the concentrations of P, K, Ca, Mg, Cu and Fe in the P_4 roots (**Table 8.3**) and P, Ca, Mg and Cu in the P_8 roots (**Table 8.12**) were significantly lower in the N_{35} and/or N_{70} rates than for N_{14}. These results suggest that as much as possible of these nutrients were being translocated from the roots to the shoots unless some mechanism was reducing the root uptake of these nutrients.

As the increasing addition of N resulted in a decrease in root dry weight production by the seedlings, the decline in nutrient concentrations in the roots was not considered to be a result of dilution as had occurred in the shoots. This was confirmed by the significant ($p<.05$) decrease in the amount of nutrients (except for N) in the roots with increasing N addition (**Tables 8.6 and 8.15**). Correlations between the root dry weights pot^{-1} and root nutrient concentrations in the roots were negative and significant for N but significantly positive for other nutrients particularly in the P_4 pot trial (**Table 8.29**). Thus with increasing root dry weight pot^{-1} the concentrations of nutrients, apart from N, also increased. As the higher root weights were associated with lower shoot weights, the shoot demand for nutrients in these seedlings may have been lower and consequently nutrient concentrations and amounts pot^{-1} in the seedling roots were able to build up or were able to be maintained at higher levels. Thus the effect of increasing N addition on root dry weights may have been indirect where N promoted shoot growth at the expense of root growth.

Table 8.29: Significant correlations (r) between the concentrations of nutrients in the root and the root dry weight pot^{-1} of radiata pine seedlings at harvest 2 of the P_4 and P_8 sand culture pot trials.

Nutrient	P_4:		P_8:	
	r	Probability	r	Probability
N ↓*	.83	.005	.88	.002
P ↑	-	-	.89	.001
K ↑	.63	.071	-	-
Ca ↑	.84	.005	.84	.005
Mg ↑	.88	.002	.79	.012
Cu ↑	.68	.043	.92	<.001
Fe ↑	.88	.002	-	-

* The direction of the arrow indicates if nutrient concentrations increased (↑) or decreased (↓) as root dry weights pot^{-1} increased.

Rook (1991) noted that a reduction in root:shoot ratios (i.e. increasing shoot:root ratios) as a result of increasing nutritional status, particularly of N, P and K, was generally accepted. According to Rook (1991) root growth is reported to be significantly affected by nutrient status which alters a) the relative allocation between root and shoot, b) the type of root, c) the absolute rates of root growth, and d) periodicity of root growth. Binkley (1986) suggested that less photosynthetic products may be allocated to fine roots when nutrient availability is greatly increased leaving more carbohydrate for stem growth. This change in C partitioning within the tree could help explain the increase in the above-ground biomass when trees have been fertilised and/or irrigated (Linder and Rook 1984).

In the P_4 and P_8 pot trials, smaller root dry weights were associated with greater total nutrient uptake (**Table 8.30**). As root dry weights increased the total uptake of N, P, K, Mg, Cu and B decreased in the P_4 and/or P_8 pot trials. The total uptake of Ca in the P_8 pot trial and Zn and Fe in the P_4 pot trial increased with increasing root dry weight. The association of smaller roots with the larger shoots suggests that these roots were more efficient in taking up nutrients as these seedlings contained the greatest total amount of nutrients (except Ca). With increasing N addition the amount of nutrient uptake per gram of root dry weight significantly increased, particularly from N_{14} to N_{35}, for all

nutrients in both pot trials (except for Zn in both P_4 and P_8 and Ca in P_8). These results are contrary to what Theodorou and Bowen (1993) found for radiata pine seedlings growing in soil. Their results indicated that N and P uptake was highly correlated with root dry weights - higher root weights were associated with greater N and P in the seedlings. This difference in the relation of root dry weights to total seedling nutrient uptake may be a reflection of the different growth media - sand culture versus soil - and therefore the difference in nutrient supply to the seedling roots. Gupta *et al.* (1985) noted that in sand culture experiments plant roots grow in a medium in which B is uniformly distributed as opposed to natural soil systems where the soil solution concentration varies in the profile. The other nutrients in the sand culture pot trial would also be uniformly distributed throughout the duration of the trials as the nutrient supply bathing the roots was being replaced frequently. The size of these root systems may not be as critical to seedling growth and nutrient uptake, as the roots do not have to exploit the media in search of nutrient supplies as happens in soil.

Table 8.30: Significant correlations (r) between root dry weight pot^{-1} and total nutrient uptake pot^{-1} of radiata pine seedlings at harvest 2 of the P_4 and P_8 sand culture pot trials.

	P_4:		P_8:	
	r	Probability	r	Probability
N ↓*	.85	.004	.87	.002
P ↓	-	-	.79	.011
K ↓	-	-	.66	.052
Ca ↑	-	-	.73	.025
Mg ↓	-	-	.80	.009
Cu ↓	-	-	.61	.084
Zn ↑	.66	.054	-	-
B ↓	.85	.004	.58	.102
Fe ↑	.96	<.001	-	-

* The direction of the arrow indicates if total nutrient uptake increased (↑) or decreased (↓) as root dry weights pot^{-1} increased.

Plants can adapt to the localised N supply by increasing the rate of N uptake per unit root weight of length and by increased root growth in an N-rich zone (Haynes 1986a). The results from the sand culture pot trials suggest that the roots of radiata pine seedlings with a high shoot:root ratio are able to compensate for the reduced rooting capacity by increasing the efficiency of nutrient uptake. Thus in sand culture a radiata pine seedling could have a higher shoot:root ratio than the equivalent seedling grown in soil without detrimental effects on shoot growth and nutrition. It also suggests that nutrient uptake from solution culture experiments and subsequent seedling growth and nutrition may not reflect 'field conditions'.

The number of epicorms per seedling and branches per seedling were significantly increased by increasing the rate of N addition from 14 to 35μg ml^{-1} in both the P_4 and P_8 pot trials. Birk (1990) noted that in glasshouse and field trials, high N levels have promoted branch growth at the expense of main stem growth. This relationship of N with branch size has been known for a long time in the field (J.A. Adams, Pers. Comm. 1993).

In the P_4 and P_8 pot trials the number of branches and epicorms on each seedling were known but not their corresponding weights as only the shoot weight pot^{-1} was measured which included epicorms and branches. From N_{14} to N_{70}, the shoot dry weight pot^{-1} increased by 54 and 49% in the P_4 and P_8 pot trials respectively. The corresponding increase in actual seedling height was only 12 and 10% respectively. These results indicate that, per unit of height, the seedlings grown with N_{70} were heavier than those with N_{14}. The correlations between shoot dry weight pot^{-1} and the average number of epicorms per seedling were positive and highly significant in the P_4 ($r=.95$, $P<.001$) and P_8 ($r=.97$, $P<.001$) pot trials. In the P_4 pot trial, the number of branches per seedling was also positively and significantly correlated with shoot dry weights pot^{-1} ($r=.69$, $p=.039$). These results suggest that an increase in the production of epicorms and, to a lesser extent, branches per seedling as N addition increased, may have reduced the proportional increase in actual seedling height.

In those seedlings where shoots represented the greater proportion of total dry weight one would expect to find the greatest proportion of nutrients. With increasing N addition the % of total nutrients located in the shoots was significantly increased (**Tables 8.9 and 8.18**) and could be attributed to an increasing proportion of the total dry weight being represented by the shoot for the N_{35} and N_{70} treatments. In the P_4 pot trial the significant increase in the % of K, Mg, Cu, B and Fe from N_{35} to N_{70} followed the increase in the shoot dry weights as a % of the total dry weight of the seedlings pot^{-1}. However the major % increase in the shoots occurred from N_{14} to N_{35}. In the P_8 pot trial most of the significant increases in the % of nutrient in the shoot followed the significant increase in the shoot as a % of the total dry weight i.e. N_{14} to N_{35}. Only K, Ca and Mg also showed a significant increase from N_{35} to N_{70}.

Haynes and Goh (1978) suggested that there was some evidence that ammonium nutrition could inhibit the translocation of cations but that does not appear to have occurred in these pot trials as the amounts of K, Ca and Mg did not significantly decline with the increasing addition of N (**Tables 8.6 and 8.15**).

If the increase in shoot dry weight, in response to increasing N, results in a significant dilution of some nutrients within the shoot as well as an increase in translocation of nutrients from the roots, does the total uptake of nutrients into the seedling change? Theodorou and Bowen (1993) found that the total oven dry weight of radiata pine seedlings was highly significantly correlated to N and P uptake where the higher uptake of N and P was associated with greater seedling growth. This also occurred in both the P_4 and P_8 pot trials (**Table 8.31**) where the uptake of a number of the other measured nutrients were also significantly correlated with total seedling dry weight. In the P_4 pot trials the correlations were all positive however in the P_8 pot trial the uptake of Ca decreased as seedling total weight increased (**Figure 8.34**). There was no such significant correlation for the P_4 pot trial where the amount of N in the shoots was significantly less (**Table 8.23b**) than in the P_8 pot trial. In the P_8 pot trial the correlations between the concentrations of N and Ca were significant and negative in the shoots ($r=.90$, $p=.001$) and in the roots ($r=.95$, $P<.001$) - as the concentration of N increased, Ca decreased. The equivalent correlations in the P_4 pot trial were not significant in the shoots but were in the roots ($r=.89$, $p=.001$).

These results suggest that with increasing N uptake the amount of Ca taken up by the seedling decreased. This was confirmed by the significant correlation ($r=.71$, $p=.034$) between increasing total N uptake with decreasing total Ca uptake in the P_8 seedlings. The plant uptake of cations such as K^+ and Ca^{2+} can be inhibited by NH_4^+ nutrition and is attributed to ionic competition during cation uptake with NH_4^+ ions or with the H^+ ions excreted during the active uptake of NH_4^+ (Haynes 1986a). However in the P_4 and P_8 pot trials the uptake of K and Mg was not inhibited by increasing

N uptake - the correlation between both total K and total Mg and total N uptake was significant and positive in both pot trials.

Table 8.31: Significant correlations (r) between total seedling dry weight and total nutrient uptake pot^{-1} of radiata pine seedlings at harvest 2 of the P_4 and P_8 sand culture pot trials.

Nutrient	P_4: r	Probability	P_8: r	Probability
N ↑*	.94	<.001	.99	<.001
P ↑	.64	.063	.96	<.001
K ↑	.91	<.001	.64	.066
Ca ↓	-	-	.71	.034
Mg ↑	.85	.004	.94	<.001
Cu ↑	.86	.003	.62	.078
B ↑	.70	.035	.72	.030
Fe ↑	-	-	.75	.020

* The direction of the arrow indicates if total nutrient uptake increased (↑) or decreased (↓) as total seedling dry weights pot^{-1} increased.

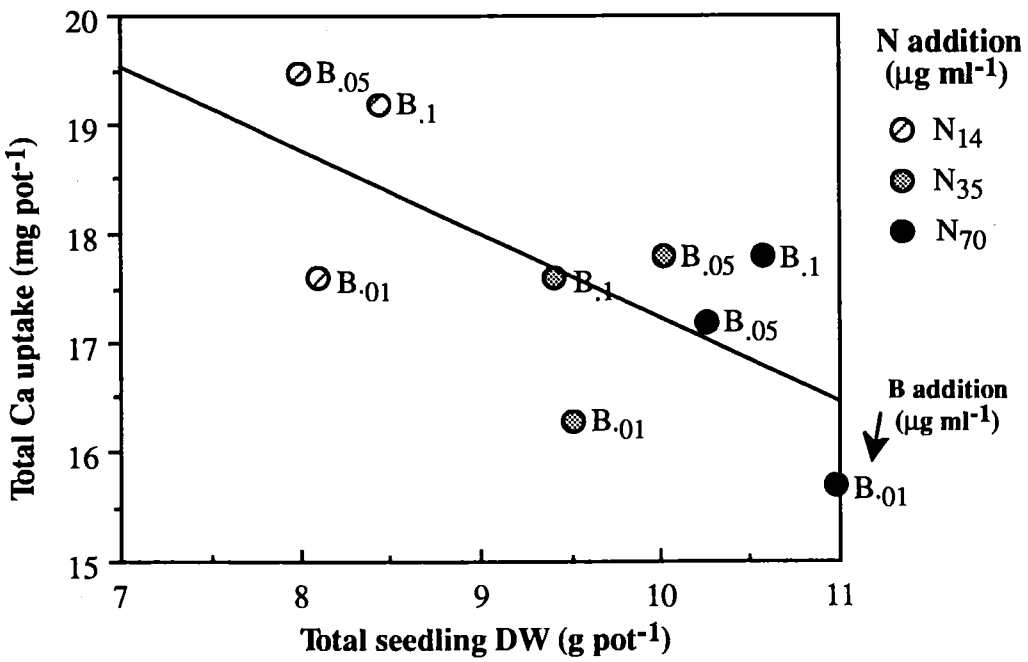

Figure 8.34: Correlation between the total radiata pine seedling dry weight and total Ca uptake per pot in the P_8 sand culture pot trial at harvest 2 ($r = .71$, $p = .034$).

Plants grown with ammonium-N generally contain higher levels of P and S than those supplied with nitrate alone (Haynes and Goh 1978). In both pot trials, particularly P_8, the total uptake of P was significantly and positively correlated with total N uptake. Sulphur was not measured in this pot trial.

Unpublished results of Bowen (1992, cited by Theodorou and Bowen 1993) suggested that a lower nutrient uptake frequently leads to a better efficiency. This was observed in the P_4 and P_8 pot trials. The increased addition of N promoted seedling shoot growth but the amount of uptake of some nutrients did not increase proportionally resulting in the dilution of those nutrients. The physiological use efficiency of these diluted nutrients, particularly P and Ca in the P_4 pot trial (**Table 8.10**) and Ca and B in the P_8 pot trial (**Table 8.19**) was therefore significantly increased by increasing the rate of N addition. According to Theodorou and Bowen (1993) the efficiency in the use of nutrients may be related to the % of total seedling nutrient translocated to the shoot and their use in photosynthesis. Thus the larger shoots had been able to grow with proportionally less of some nutrients (as noted above for the P_4 and P_8 pot trials), without a decline in dry weight production, by more efficiently using those nutrients during the growth processes.

At harvest 2, the addition of N had a significant effect on the seedling physical measurements of seedling pot height (P_4 pot trial only), actual seedling height, seedling height difference, the number of epicorms/seedling and the number of branches/seedling.

The seedlings in **Plates 4a and 4b** illustrate the degree of deviation of growth from a straight stem. It was assumed that the height difference reflected the amount of height lost due to the kinking and sideways growth of the seedling stem and, as such, was a simple measure of the amount of stem deformity.

It was assumed that the environmental conditions (such as temperature, light and air movement) within the glasshouse would affect the seedlings equally - particularly as the treatments were blocked so that treatment replicates were spatially spread out within each pot trial. Thus any significant differences observed in the degree of deformity of the seedlings could be attributed to the nutrient additions. It was thought that the investigation of the causes of height difference in the seedlings, during the pot trial, may help to explain the stem deformities observed in radiata pine trees in the field.

As most of the seedlings in both pot trials exhibited some form of stem deformity the cause was thought to arise from the fast growth rate of the seedlings encouraged by a combination of warm temperatures in the glasshouse and the high availability of nutrients and water from the sand culture solution.

The increasing addition of N from 14 to 35μg ml^{-1} significantly promoted seedling growth mainly in terms of shoot dry matter production. Actual seedling height and shoot dry weight pot^{-1} were positively and significantly correlated for both the P_4 ($r=.89$, $p=.001$) and P_8 ($r=.97$, $p<.001$) pot trials. Actual seedling height and the height difference per seedling were also significantly and positively correlated for both the P_4 ($r=.88$, $p=.002$) and P_8 ($r=.81$, $p=.008$) pot trials. Thus the larger seedlings, promoted by the higher additions of N, also had the greater height difference (see **Figures 8.4 and 8.11**) and therefore a greater level of stem deformity.

Correlations were used to identify any particular nutrient or nutrient:N ratio that may have been responsible for the variation in height difference. The shoot concentrations of N, Ca, B and Zn, in the P_4 pot trial, and N, B and Fe, in the P_8 pot trial, were significantly correlated with seedling height difference (**Table 8.32**).

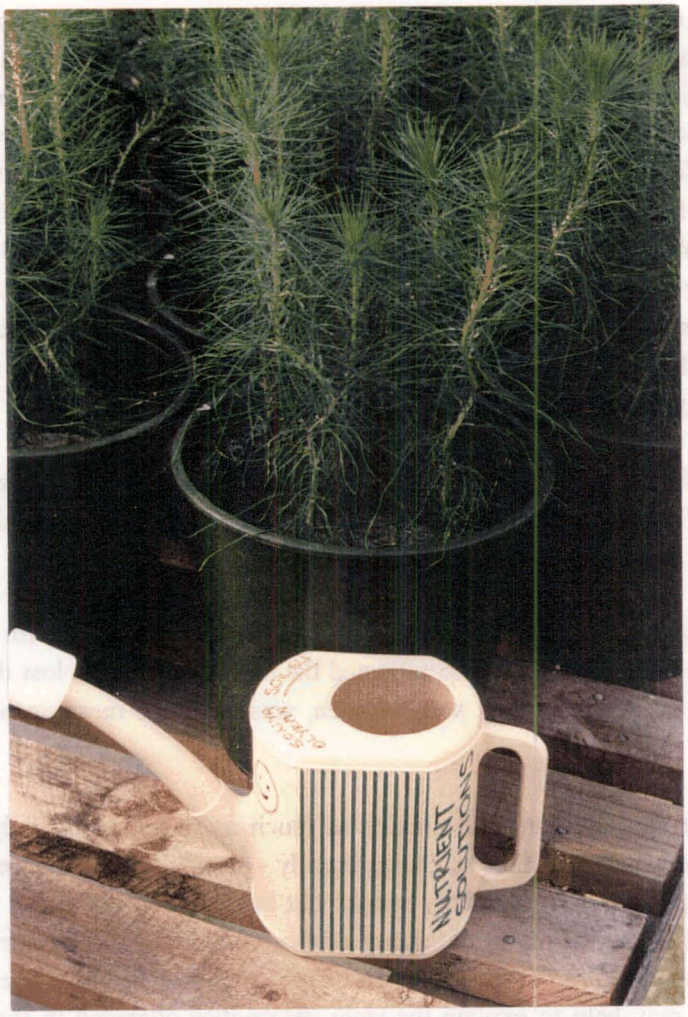

Plate 4a

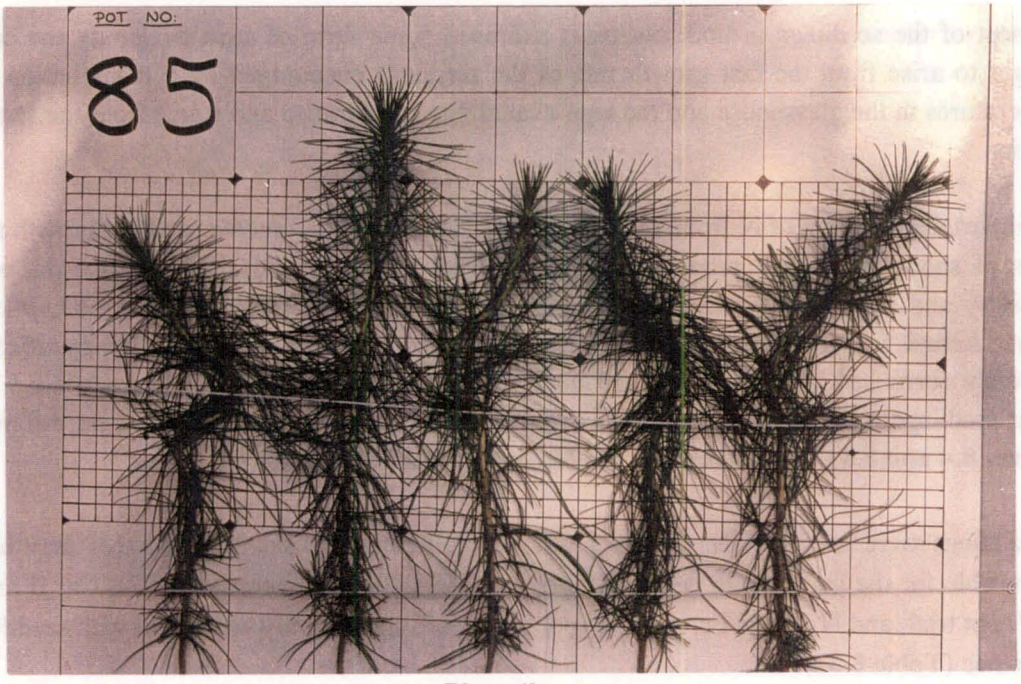

Plate 4b

Plate 4: Stem deformities of radiata pine seedlings grown in sand culture pot trials in the glasshouse: a) prior to harvest 2 and b) at harvest 2.

Table 8.32: Significant correlations between seedling height difference and nutrient concentrations in the shoots of radiata pine seedlings at harvest 2 of the P_4 and P_8 sand culture pot trials.

Nutrient	P_4: r	Probability	P_8: r	Probability
N ↑*	.73	.025	.77	.015
Ca ↓	-	-	.89	.001
Zn ↓	.62	.075	-	-
B ↓	.63	.075	.67	.049
Fe ↑	-	-	.83	.006

* The direction of the arrow indicates if nutrient concentrations increased (↑) or decreased (↓) as seedling height difference increased.

In both pot trials many of the nutrient:N ratios were significantly correlated with seedling height difference where an increase in the nutrient:N ratio was associated with a decrease in the height difference. These results, and the correlation of nutrient concentrations with height difference, may be a reflection of the effect of N increasing seedling shoot weight and height which promoted nutrient dilution (i.e. reduced nutrient concentrations and nutrient:N ratios) and increased the amount of height difference in the seedlings (this effect depended on the rate of B addition as shown in **Figures 8.4 and 8.11**). Because N was so dominating in its effect on the seedling shoot growth it appears that the resulting dilution of one or more of the other nutrients may have been the cause of the height difference.

Nitrogen, among the macronutrients, has the most important effect on the plant uptake of B (Gupta *et al* 1985). Of the significant correlations between nutrient concentrations and height difference in the 2 pot trials the ones in common were N and B (**Table 8.32**). In both pot trials as the shoot concentration of N increased so did the height difference (**Figure 8.35a**) while with increasing B concentrations the height difference declined (**Figure 8.35b**). However the correlation between B:N ratios in the shoots and the height difference was more significant than the correlations with N or B concentrations alone (**Figure 8.35c**). These results suggest that the lower B:N ratios were associated with an increase in seedling height difference.

One of the first symptoms of B deficiency in young radiata pine, according to C.J. Borough, W.J.B. Crane, and C. Johnston (unpublished) are wavy branches and wavy main stem. The symptoms of growth deformity exhibited in the P_4 and P_8 pot trials resembled this. Such deformities may be due to the disintegration of parenchyma and other thin-walled cells which result in an observed fragility of the stem (Mayevskaya *et al* 1979, cited by Shkolnik 1984). In the P_4 and P_8 pot trials the new seedling growth may have been soft and thus prone to bending. As air movement was minimal within the glasshouse, it was possible that gravity - particularly on the larger and heavier seedlings - may have caused the seedlings to bend downward.

According to Birk *et al* (1989) and Birk (1990) growth deformity symptoms associated with B deficiency are relatively common for young radiata pine trees growing on ex-pasture sites. The results from the P_4 and P_8 pot trials suggest that, of the micronutrients measured, B appeared to be the only one that was associated with the measurements of stem deformity in the radiata pine seedlings grown in sand culture.

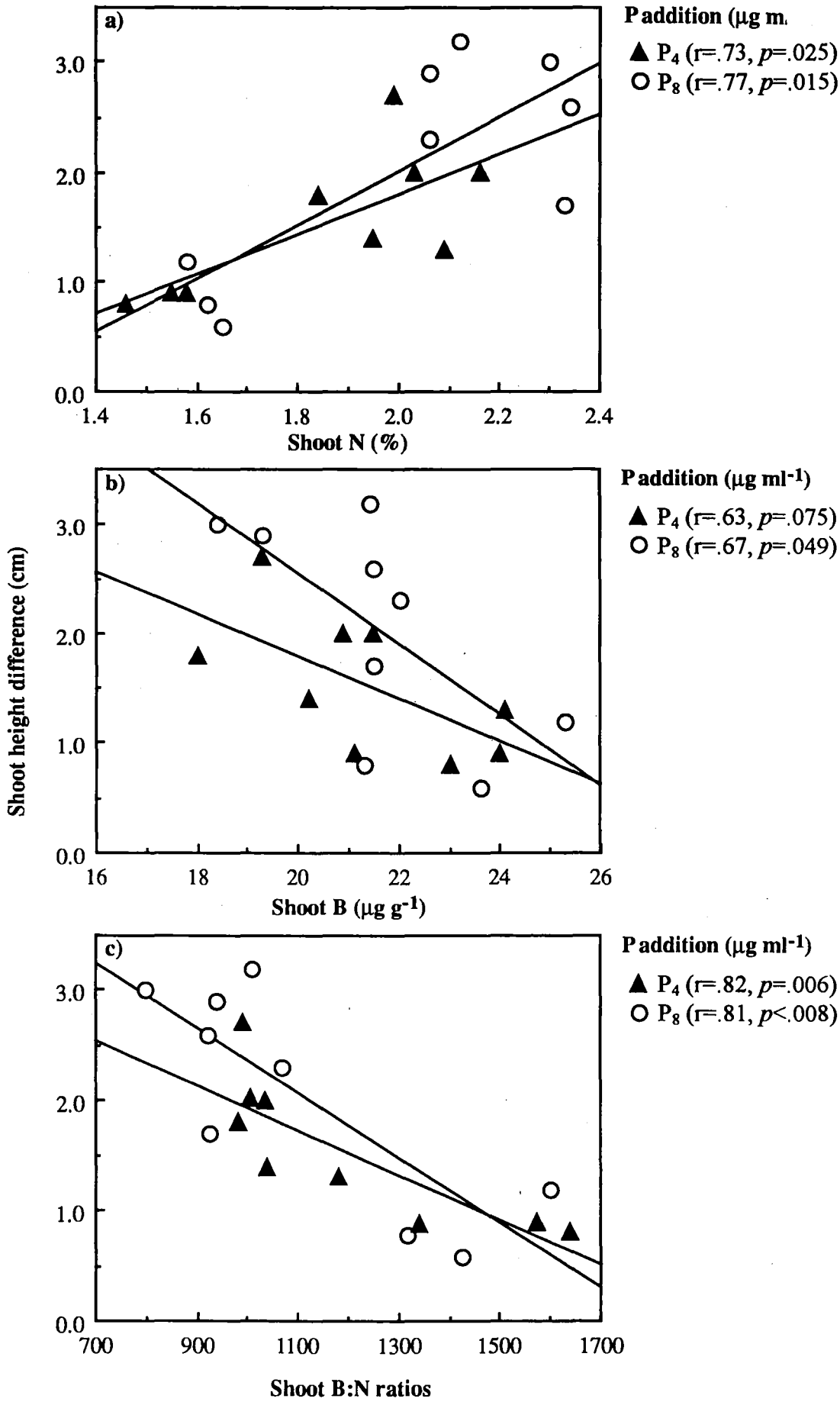

Figure 8.35: Correlation between seedling height difference and a) shoot N concentrations, b) shoot B concentrations and c) shoot B:N ratios of radiata pine seedlings in P_4 and P_8 sand culture pot trials.

8.4.2.2 The effect of B addition

The effect of B addition in the two pot trials was less significant than that of N - even for the concentrations and amount of B in the seedling shoots where N addition was often more significant in decreasing them than the effect of increasing B addition was in increasing them. A similar situation occurred in the Ashley field trial where N addition significantly affected many of the measured nutrient concentrations while B addition only significantly changed the concentrations of B (Chapter 4).

There were four measurements, all involving seedling B, that were significantly ($p<.10$) affected by the increasing addition of B in both pot trials: the concentration of B in the shoots and roots, B:N ratios in the roots and the amount of B in the roots pot^{-1} **(Table 8.33)**. Across the two pot trials these measurements were not significantly affected by the rate of P addition or an interaction between P and B. The trends in both pot trials were similar - with increasing B addition, or as the rate of B addition increased from 0.01 to 0.1 or 0.01 to 0.05μg ml^{-1}, the B measurements significantly increased.

The effect of B addition on B concentrations showed as a clear pattern in the seedling roots, but was less obvious in the shoots in the P_4 and P_8 pot trials. In the roots of the P_4 and P_8 seedlings, B concentrations significantly increased as B addition increased from $B_{.01}$ to $B_{.1}$ **(Tables 8.3 and 8.12)**. The difference between the shoots and roots appeared to be related to the significance of N in affecting B concentrations in the shoots and the absence of any significant N effect in the roots where the addition of B was highly significant.

Marcos de Lanuza (1966, cited by Stone 1990) grew radiata pine seedlings in water culture containing 0.005 to 0.5μg l^{-1} of B. The resulting B concentrations ranged from 23 to 44, 8 to 18 and 4 to 11μg g^{-1} in the total foliage, stem and roots respectively. In the P_4 and P_8 pot trials the range of B supplied varied 10-fold from 0.01 to 0.1μg l^{-1} and resulted in corresponding concentration ranges of 20 to 23 and 9 to 13μg g^{-1} in the shoots (foliage and stem) and roots respectively. Such results, where a large-fold increase in the solution concentrations of B result in only a small-fold increase in the plant B concentrations, suggest a large measure of plant control over B uptake (Stone 1990).

There was no consistent effect of B addition on seedling growth in the pot trials. C.J. Borough, W.J.B. Crane, and C. Johnston (unpublished) suggested that B deficiency reduced rooting but the only significant effect of B addition on root dry weight occurred in the P_4 pot trial where an increase in the rate of B from $B_{.01}$ and $B_{.05}$ to $B_{.1}$ resulted in a significant decrease in root dry weight production (2.2 and 2.2g pot^{-1} to 2.0g pot^{-1} respectively).

The addition of B affected a number of other seedling growth and nutrient measurements **(Table 8.33)**. However, the effect was only significant in one of the pot trials and not in both (e.g. seedling growth measurements in P_4, Ca and Zn concentrations in the P_8 roots, P_8 shoot B:N ratios etc.) and are therefore discussed later in this chapter.

Table 8.33: Effect of added B and the probability of a significant B main effect (Prob. of B, NS = not significant) on radiata pine seedling physical and nutrient measurements in the P_4 and P_8 pot trials and an indication of whether the addition of P (P) and the interaction between added P and B (P*B) was significant (✓) or not (×), at $p<.10$, across the two pot trials at harvest 2. For each measurement in each pot trial, means with the same letter were not significantly different at $p<.05$ or, if the letters were bracketed, at $p<.10$. Shaded areas indicate a measurement that was significantly affected by B addition in both pot trials.

	P4:				**P8:**					
	Prob. of B	B rate (μg ml^{-1}) $B_{.01}$	$B_{.05}$	$B_{.1}$	Prob. of B	B rate (μg ml^{-1}) $B_{.01}$	$B_{.05}$	$B_{.1}$	P	P*B
Seedling growth:										
Shoot DW	.030	a	ab	b	NS	-	-	-	×	×
Root DW	.088	(a)	(a)	(b)	NS	-	-	-	✓	×
Actual seedling height	.056	a	ab	b	NS	-	-	-	✓	×
No. epicorms/seedling	.071	(a)	(a)	(b)	NS	-	-	-	✓	×
Nutrient concentrations:										
Shoot B	.021	b	ab	a	.003	b	a	a	×	×
Root B	<.001	c	b	a	<.001	c	b	a	×	×
" Ca	NS	-	-	-	.037	a	ab	a	✓	×
" Zn	NS	-	-	-	.021	ab	b	a	×	✓
Nutrient:N ratios:										
Shoot B:N	NS	-	-	-	.004	b	a	a	✓	×
Root B:N	<.001	b	a	a	<.001	c	b	a	×	×
" Zn:N	NS	-	-	-	.075	ab	b	a	×	×
Amount of nutrient pot^{-1}:										
Shoot B	NS	-	-	-	.009	b	a	a	×	×
" K	.087	a	ab	b	NS	-	-	-	×	✓
" Ca	.063	a	a	b	NS	-	-	-	✓	✓
Root B	<.001	b	a	a	.001	b	a	a	×	×
" Zn	NS	-	-	-	.021	ab	b	a	✓	✓
Total nutrient pot^{-1}:										
B	NS	-	-	-	.002	b	a	a	×	×
K	.052	a	ab	b	NS	-	-	-	×	✓
Ca	.038	ab	a	b	NS	-	-	-	×	✓
Zn	NS	-	-	-	.013	ab	b	a	✓	✓
% of nutrient in shoots:										
B	.021	a	ab	b	NS	-	-	-	✓	×
Zn	NS	-	-	-	.020	ab	a	b	✓	✓
Root uptake efficiency:										
B	.014	b	b	a	NS	-	-	-	✓	×
Zn	NS	-	-	-	.021	ab	b	a	×	✓
Physiological efficiency:										
B	.027	a	ab	b	.003	ab	b	a	×	×

8.4.2.3 The effect of P addition

As the two pot trials only differed in the rate of P being applied, any differences in seedling growth or nutrition between the two trials could be a result of the rate of P addition or an interaction between the rates of added P and the rates of N or B.

From the literature, the rates of P that have been added in solution for radiata pine seedling growth vary greatly. For instance, Taber and McFee (1972) found that adequate P was absorbed by radiata pine seedlings from a solution containing 0.75 to 0.007μg ml^{-1}. Truman *et al* (1986) grew radiata pine seedlings in nutrient solutions where P was applied at two 'low' levels of 1 and 3μM l^{-1} (equivalent to 0.031 and 0.093μg of P ml^{-1}) and at three 'high' levels of 18, 32, 129μM l^{-1} (equivalent to 0.56, 0.99 and 4.0μg of P ml^{-1}). The highest of the P rates added by Truman *et al* (1986) is the same as the lower rate of P (4μg ml^{-1}) which was added in the P_4 sand culture pot trial. In the literature, the highest rate of P addition for radiata pine seedlings grown in solution culture was 8μg ml^{-1} (Adams and Attiwill 1982) which was also the rate of P added in the P_8 sand culture pot trial.

Generally, the nutrients in both pot trials, apart from P, behaved in a similar fashion - particularly following the addition of N where the promotion of shoot dry weights resulted in the dilution of other nutrient concentrations. However, when comparing the P_4 and P_8 pot trials, there were a number of differences in the nutrient and seedling growth data.

The major difference between the two pot trials at harvest 2 was in the effect of the rate of P addition on P concentrations, P:N ratios, the amount of P in the shoots and roots pot^{-1} and the amount of total P pot^{-1}. In all cases these were higher in the P_8 pot trial so that the total amount of P in the seedlings, at 35.8mg pot^{-1} was 43% higher than the 25.0mg pot^{-1} for the P_4 pot trial. However, a number of these measurements were also affected by a significant interaction between added P and N. In the P_4 pot trial increasing N addition resulted in a significant decrease in shoot P concentrations (**Figure 8.16**) which did not occur in the P_8 pot trial where the increasing addition of N was not significant. In the P_4 pot trial the concentrations of P in the shoot appear to have been more vulnerable to the negative effect of N on P that was also observed in previous work with radiata pine (Ashley and Taheke field trials) so that the dilution of P concentrations occurred as increasing N addition promoted shoot growth. However, in the P_4 roots (**Figure 8.17b**) the P concentrations declined, but not significantly, while the decline in the P_8 root P concentrations was significant although the root P concentrations were much higher than those for the P_4 roots. The decrease in P concentrations in the roots were most likely the result of an increasing percentage of the P being found in the shoots with increasing N addition - this was particularly noticeable in the P_8 shoots (**Table 8.18**).

Another example of P concentrations in the P_8 pot trial being able to resist the negative effect of N addition was observed for shoot P:N ratios (**Figure 8.18**). In both pot trials P:N ratios significantly declined with increasing N but the ratios in the P_8 pot trial were, for all rates of N addition, significantly higher than for P_4. This effect was particularly evident in the roots (**Figure 8.19a**) where the P:N ratio for P_8N_{70} was not significantly different from P_4N_{14}.

The amount of P in the shoots significantly increased with increasing N particularly for the P_8 pot trial. As P concentrations did not decline with increasing N, the increase in P amounts was a simple function of the promotion of shoot growth by increasing N addition and the ability of the seedlings to maintain P uptake at the higher P_8 rate. The amount of P in the roots significantly declined in each pot trial with increasing N from 14 to 35μg ml^{-1} (**Figure 8.23a**) - and may reflect the greater increasing shoot demand for P and consequently the greater % of P found in the shoots for both pot trials. The amount of total P in the seedlings was significantly affected by increasing N addition in

the P_8 pot trial but not in the P_4 pot trial. The effect was positive in both pot trials but more obvious for P_8 (**Figure 8.25a**). Taber and McFee (1972) also found that an increase in P concentration in solution stimulated N and P uptake by radiata pine seedlings.

At harvest 2 the rate of P addition did not significantly affect the seedling shoot and root dry weights pot^{-1} (**Table 8.20**) however the shoot:root ratios were significantly ($p<.05$) higher in the P_8 pot trial. As the addition of P was not significant for the total dry weight of the radiata pine seedlings, which was 9.5g pot^{-1} for both pot trials, the effect of P_8 on the shoot and root dry weights was due to a change in the allocation of dry matter production between the shoots and the roots.

The P_8 seedlings had significantly taller pot heights and actual heights. Truman *et al* (1986) found that there was a significant height response by radiata pine seedlings to increasing 'higher' levels of P. The average height difference of 2.0 cm for the P_8 pot trial was significantly ($p<.10$) higher than the 1.5 cm for the P_4 pot trial - the significance was calculated by Anova on the squareroot transformation of the original data which was skewed due to several high values. Over the two pot trials the height difference ranged from 0 to 13.8cm.

The effect of P on seedling growth was 'extra' to that due to N and B and was not a result of any interactions between P and N or B. However, when the two pot trials were statistically analysed together, to test for the effect of P, the rates of increasing N addition still explained a greater proportion of the data variation than P or B (**Table 8.34**). The order of significance of the treatment nutrients was generally N>P>B for seedling growth. For the measurements of seedling height and the number of branches and epicorms per seedling, a large proportion of the data variation was not explained by the rates of N, P or B addition.

Table 8.34: Percentage of data variation (sums of squares) explained by N, P, or B addition when the P_4 and P_8 pot trials were statistically analysed together in an Anova.

	% Sum of Squares explained by treatment		
Seedling growth parameter	N	B	P
Shoot dry weight pot^{-1}	80.3	1.5	0.3
Root dry weight pot^{-1}	41.0	2.4	4.8
Shoot:root ratio	82.4	0.7	3.0
Seedling pot height	2.8	0.3	1.6
Actual seedling height	12.4	1.2	4.0
Height difference*	15.4	0.8	1.3
No. epicorms $seedling^{-1}$	14.8	0.4	3.8
No. branches $seedling^{-1}$	4.9	0.4	0.1

* Based on the variation in the transformed (squareroot) data.

Apart from the effect of the two rates of P addition on P dynamics in the seedling there were also significant differences between the two pot trials for the shoot concentrations of N, Cu and Fe (**Table 8.21b**), Cu:N and Fe:N ratios in the shoots and Ca:N ratios in the roots (**Table 8.22**), the amount of N, Mg and Cu in the shoots pot^{-1} and the amount of Ca in the roots pot^{-1} (**Table 8.23b**)

and the total amount of N and Cu pot^{-1} (**Table 8.24**). None of these nutrient measurements were affected by a significant interaction between P and N or B.

In the shoots, N and Cu seemed to be the nutrients that were most affected by the two rates of P addition. In general at harvest 2, the concentration and amount of N in the shoots was significantly higher in the P_8 pot trial while Cu was significantly lower in the P_8 pot trial than for P_4. The total amount of N was significantly higher in the P_8 seedlings. As the mean total seedling weight was the same for both P rates, the seedlings in the P_8 pot trial took up proportionally more N than in the P_4 pot trial. This was located in the shoots (**Table 8.23b**) and accounted for the significantly higher concentrations and amounts of N in the P_8 shoots. The 81.7% of the total seedling N found in the shoots of the P_8 seedlings was significantly ($p<.05$) higher than the 79.4% for the P_4 seedlings. These results indicate that P promoted the seedling uptake of N which in turn may have resulted in the larger seedling shoots in the P_8 pot trial.

Significantly less total Cu pot^{-1} was taken up by the P_8 seedlings (**Table 8.24**). As a result, significantly less Cu was found in the shoots of the P_8 seedlings (**Table 8.23b**) while the amount and concentration of Cu in the seedling roots was not significantly different. These results suggest that the higher rate of P addition reduced the translocation of Cu to the shoots of the P_8 seedlings (as indicated in **Table 8.26**) where the % of total Cu in the shoots was less for the P_8 seedlings. According to Jarvis (1981) an increased supply of P from the soil may restrict Cu transport from the roots to the shoots. However, in the P_8 pot trial the rate of P addition was not significant for the % of total Cu found in the seedling shoots.

Pederick *et al.* (1984) found that the foliar concentration of Cu in radiata pine was directly related to P levels which were particularly high and typical of those from trees growing on ex-agricultural soils which had received phosphorus fertiliser. Raupach *et al* (1978) found that high P levels were associated with high micronutrient levels in radiata pine growing on ex-farm land.

Both the shoot concentration of Fe and the Fe:N ratios were significantly lower in the P_8 seedlings. As the shoot amount of Fe was not significantly different between the two pot trials, dilution due to the greater P_8 seedling dry weights may account for the lower Fe in these P_8 shoots.

The amount of Ca and Ca:N ratios were significantly less in the P_8 roots. However the total amount of Ca pot^{-1} was not significantly different in the P_4 and P_8 seedlings. It seems that the rate of P addition was highly significant ($p<.001$) for the % of total Ca located in the shoots - the P_8 shoots contained 75.5% of the seedling Ca while the P_4 shoots had 71.6%. The higher rate of P addition favoured Ca transport to the shoots at the expense of Ca in the roots. Also in the P_8 pot trial the increasing addition of N was not significant for the amount of Ca in the shoots but N was significant for the amount of Ca in the P_4 shoots.

Soil Bray P, in an ex-pasture system in New Zealand where radiata pine is grown, has been found at high levels (see **Tables 3.9a and b**). The effects of increasing P in the sand culture pot trials on radiata pine seedlings may therefore be of some relevance to the effect of high P levels on nutrient interactions in agroforestry systems.

8.4.2.4 Different effects of N in the 2 pot trials

A number of nutrient measurements, while not significantly affected by the rate of P addition, were significantly affected by the interaction between added N and P - i.e. the effect of N on the nutrients depended on the rate of P addition. This was particularly noticeable in the seedling roots (**Figure 8.17**) where the differences in the effect of N in the two pot trials did not follow any common trend and was quite nutrient specific.

The effect of increasing N addition in reducing Fe:N ratios in the roots was less significant for the P_8 seedlings (**Figure 8.19c**) compared to the large decreases with increasing N in the P_4 roots. This trend exhibited by the Fe:N ratios reflects the response of the amount of Fe in the roots which was also affected by a significant interaction between N and P (**Figure 8.23b**). This may have been a result of the significant (p=.055) interaction of P and N on the % of total Fe in the seedling shoots. As N addition increased in the P_4 pot trial the % of Fe in the shoots significantly increased (**Table 8.9**). However in the P_8 pot trial there was no significant difference between the effect of the N_{35} and N_{70} rates on Fe % in the shoots (**Table 8.18**) which may explain why there was no significant difference between N_{35} and N_{70} on Fe:N ratios and the amount of Fe increased from N_{35} to N_{70} in the P_8 roots.

The interaction between P and N was also significant for the total amount of Fe pot^{-1} (**Figure 8.25b**). In the P_4 pot trial the total amount of Fe significantly decreased from N_{14} to N_{70} while in the P_8 pot trial the amount of Fe increased from N_{14} to N_{70}. The addition of N in the P_8 pot trial did not significantly affect the total amount of Fe in the seedling but did in the P_4 pot trial.

8.4.2.5 Different effects of B in the 2 pot trials

The effect of B on seedling growth and nutrition was generally different in the two pot trials. In the P_4 pot trial at harvest 2, seedling growth measurements were significantly and negatively affected by increasing B addition - from $B_{.01}$ to $B_{.1}$ or $B_{.05}$ to $B_{.1}$ - while in the P_8 pot trial this did not occur (**Table 8.33**). Differences between seedling growth parameters in the P_8 pot trial were generally more significantly the result of increasing N addition. In the P_8 pot trial, B addition had a more significant effect on the concentrations and amounts of B and B:N ratios in the shoots, the total amount of B in the seedlings, and the physiological efficiency of B use - all these measurements significantly increased with increasing B addition. In the P_4 pot trial B addition was significant for the % of B in the shoots, which decreased with increasing B, and the efficiency of B uptake by the root which increased with increasing B.

A number of other nutrient measurements, apart from B, reacted differently to B addition depending on the rate of P addition - shoot and total K and Ca in the P_4 pot trial and Ca concentrations in the root and a number of Zn measurements in the P_8 pot trial were all significantly affected by B addition.

In general it appeared that the significant effects of increasing B addition which only occurred in the P_4 pot trial were negative (except for the root efficiency of B uptake). In contrast, they were positive (except for the % of Zn in the shoots) in the P_8 pot trial. It is difficult to describe the relationship between P and B - for some of the measurements significantly affected by B, the rate of P addition was also significant and yet others were affected by a significant interaction between P and B. However, there did not appear to be any common trends in these responses.

8.5 CONCLUSIONS

Harvesting the radiata pine seedlings at 6 months of age, 4 months after the treatment nutrient solutions had been added to the sand culture pot trials, allowed sufficient time for the N and B treatments to significantly affect many of the measured growth and nutritional characteristics of the radiata pine seedlings.

The addition of rates of N had a greater significant effect on seedling growth and nutrition in the two pot trials than the addition of B. The major effects of increasing rates of N addition are described in the following list:

1) Increasing the rate of N addition significantly increased the total uptake of N into the radiata pine seedlings. The concentration and amount of N in the shoot significantly increased with increasing N addition in the P_8 pot trial but in the P_4 pot trial the increases in N% and amount were only significant from N_{14} to N_{35}. Higher N concentrations in the shoot appeared to increase shoot weight as these two measurements were positively and significantly correlated in the two pot trials. This was most evident as N addition increased from 14 to 35μg ml^{-1}. The increase in shoot growth was significantly correlated with a decline in the shoot concentrations of B, Ca and P, in the P_4 pot trial, and Ca, Zn and B in the P_8 pot trial. It was found that increasing N addition from 14 to 70μg ml^{-1} resulted in the dilution of P (P_4 only) and Ca in the shoots while an increase from 14 to 35μg ml^{-1} significantly diluted shoot B concentrations in both pot trials. In the P_8 pot trial however, increasing N addition did not have a significant effect on the shoot concentrations of Zn.

2) An increase in the number of epicorms per seedling may have accounted for the proportionally lower increase in actual seedling height compared to the proportional increase in shoot dry weight.

3) With increasing N addition, particularly from 14 to 35μg ml^{-1}, a greater proportion of the total nutrient content of the seedling was located in the shoots. As a result, there was a decrease in the amount and concentration of most nutrients (apart from N) in the roots as the rate of N increased or as the rate increased from 14 to 35 or 14 to 70μg ml^{-1} depending on the nutrient.

4) As N addition increased from 14 to 70μg ml^{-1}, root dry weights significantly decreased in the P_4 pot trial but N addition had no significant effect on the P_8 root dry weights. In both pot trials the shoot:root ratios significantly increased from N_{14} to N_{35}. This was mainly due to the significant increase in shoot dry weights between these two rates. To compensate for these changes there was an increase in the efficiency of P, K, Mg and Cu uptake in both pot trials, and Ca in P_4 and B in P_8, by the seedling roots as N addition increased from 14 to 35μg ml^{-1}. The efficiency of N uptake in both pot trials, and B in P_4 and Fe in P_8, increased with increasing N addition. The efficiency of Zn uptake was not affected by increasing N rates in either pot trial.

5) There was a decrease in the physiological efficiency of N use as N addition increased in the P_8 pot trial and a decrease in N (P_4 pot trial), Cu (P_8 pot trial) and Fe use as N addition increased from 14 to 35 μg ml^{-1}. For the other nutrients (apart from K) there was generally an increase in their physiological efficiency of use as N addition increased although when the significant change occurred (ie between which rates of N) depended on the nutrient and the pot trial.

6) There was an increase in the height difference of the seedlings with an increase in N addition from 14 to 35 μg ml^{-1} in both pot trials based on transformed data. The increase in seedling height difference was significantly correlated with increasing shoot N concentrations, decreasing shoot B

concentrations and particularly a decrease in B:N ratios in the shoots.

In both the P_4 and P_8 pot trials the increasing addition of B increased B concentrations in the shoots and roots, B:N ratios in the roots, and the amount of B in the roots. It depended on the B measurement and the pot trial as to when a change in the rate of B caused a significant change. A number of other significant effects on seedling growth and nutrient measurements, as a result of increasing B addition, also occurred but only in one of the pot trials. These tended to be positive in the P_8 pot trial and negative in the P_4 pot trial. The actual mechanisms behind these differences was not clear.

Across the two pot trials the major effects of P addition are described in the following list:

1) In the P_8 pot trial the seedlings had a greater shoot:root ratio, taller pot and actual seedling heights and a larger number of epicorms than the P_4 seedlings.

2) P added at 8μg ml^{-1} significantly increased P concentrations, P:N ratios, the amount of P in both the shoots and roots and the total amount of P in the seedlings while the proportion of total seedling P located in the shoot was less in the P_8 pot trial. Other nutrient measurements that were higher in the P_8 pot trial included shoot N%, the amounts of shoot Zn and root Cu, Zn and Fe; the total amount of N in the seedlings, the efficiency of N, P, K, Ca, Mg and B uptake by the roots, the proportion of seedling N, K, Ca, and Mg located in the shoots; and the physiological efficiency of Cu use. Those nutrient measurements that were significantly lower in the P_8 pot trial, than in P_4, included shoot Cu and Fe concentrations and Cu:N and Fe:N ratios in the shoots, the ratio of Ca:N in the roots, the total amount of Cu in the seedlings and the physiological efficiency of N and P use.

3) It appeared that the negative effect of N addition on P in the seedlings was reduced when P was added at 8 compared to 4μg ml^{-1} mainly due to the greater amount of P present in the P_8 seedlings. There were other significant interactions between N and P particularly on nutrient concentrations in the roots. Each affected nutrient displayed a different response to increasing rates of N and P.

In general the results highlight the large effect - both physically and nutritionally - that high levels of added N have on radiata pine seedlings grown in sand culture pot trials. The addition of B, in contrast, was only significant for B measurements in both pot trials. It also appeared that high levels of added P influence radiata pine seedling growth and nutrition and may promote the uptake of N.

Chapter 9

Synthesis and conclusions

9.1 INTRODUCTION

This study began with the Taheke field trial in a young radiata pine plantation growing on an ex-pasture site. This site appeared to be ideal for rapid tree growth as the nutrient status of the soils was high from a land-use history of pasture development, the volcanic soils were deep and free-draining and the climate was warm with a high annual rainfall.

At Taheke, the predominant form of inorganic N in the soil was nitrate and the site had a high nitrification potential. This contrasted with the Whakarewarewa Forest sampling site, in a mature radiata pine plantation with a history of radiata pine production, which had less total soil N, the inorganic form of N was ammonium and the nitrification potential of the site was very low.

The radiata pine at Taheke exhibited mild amounts of stem deformity. The literature suggested that this was possibly due to high levels of soil N - particularly as nitrate which resulted in nutritional imbalances. The addition of N to this site was expected to enhance the level of stem deformity but this did not happen probably due to the high level of N that already existed in the soil.

The characteristics of the Ashley Forest trial site contrasted strongly with those at the Taheke ex-pasture site. The soils at Ashley had a lower nutrient status, the annual rainfall was low, the predominant form of inorganic N was ammonium (data not presented) and the amount of soil B was marginal for radiata pine growth. The results indicated that the amount of P and B in the soils and trees were low and these nutrients may have been limiting tree growth at Ashley. The addition of fertilisers was expected to significantly increase tree growth and change foliar nutrient concentrations and movement.

The conclusions from the field work at Taheke and Ashley were further examined in sand culture pot trials where the supply and ionic form of nutrients to radiata pine seedlings could be controlled in a favourable environment.

The first pot trial investigated the effect of the inorganic form of N on radiata pine seedling growth and nutrition. Both the literature and the field trials described here indicated that one of the major differences between ex-pasture and plantation forestry was the inorganic form of N (ammonium or nitrate) which could affect the uptake of cations and anions, nutrient balances in the shoot and, subsequently, tree growth.

The two pot trials described in Chapter 8 investigated the effect of increasing N and B at two rates of P. These nutrients had been identified as important at Ashley and P was also interesting from an ex-pasture perspective as one of the macronutrients present in high amounts in the soil.

The overall objective of the studies described here was the investigation of N, at high rates of addition, and how this altered the growth and nutritional balances, particularly in reference to micronutrients, of radiata pine in a variety of situations.

9.2 NUTRITIONAL RESPONSE OF RADIATA PINE TO FERTILISER ADDITION

During this study, the increasing addition of N significantly affected nutrient concentrations and amounts in radiata pine foliage by increasing the level of nutrient retranslocation, the translocation of nutrients to seedling shoots, the efficiency of nutrient uptake by seedling roots and the physiological efficiency of nutrient use. Indirectly, the addition of N caused nutrient dilution by increasing radiata pine growth.

Given the different soil fertility status at Taheke compared with Ashley (**Table 9.1**), one would expect the addition of N to have a much greater effect on the concentrations of N and other nutrients at Ashley. This appeared to be true for N. Although there was not much difference between the control concentrations of foliar N at Taheke and Ashley (1.8 and 1.6% respectively in fully-extended needles), at Taheke the addition of N only had a short-term effect in significantly raising foliar N concentrations (**Table 3.2**) while at Ashley, foliar N concentrations were significantly increased above the control levels, throughout the trial, particularly when N was added at 400kg ha^{-1} (**Figure 4.5**). A comparison of soil N at the two sites indicated that both total N% and the amount of mineral N were considerably higher in the Taheke soils, particularly at a depth of 0 to 10cm. The high rates of N addition at Ashley had a greater effect on foliar N concentrations because, proportionally, the addition of 400kg N ha^{-1} may have represented a large input into the forest system. This was not so for the addition of 500kg N ha^{-1} at Taheke.

At Taheke and Ashley there were a number of macronutrients, apart from N that were significantly affected by the addition of N - P, Ca and Mg at Taheke and P and Mg at Ashley. At both Taheke and Ashley the foliar concentrations of P were marginal in the control plots, compared to the standard values of Will (1985), and significantly decreased to low levels where N had been added. While the foliar concentrations of P were similar at the two sites, the amounts of Bray 2 P (extraction 1) at Taheke were at least 10 times greater in the 0 to 25cm depth and the P buffering capacity of the soils at Taheke was also greater.

There were several factors that may have reduced the uptake of P by the Taheke trees. The first is the competition for nutrients with the pasture component in the 0 to 25cm horizon and possibly in the horizons below this as well. It was noticeable, particularly in profile 2 at Taheke (**Table 3.9b**) that the amount of Bray 2 P extracted declined rapidly with increasing depth. However, the extractions down to approximately 75cm were still higher, in general, than at Ashley.

A second possibility was the effect that the form of inorganic N had on cation/anion uptake. Results from the N-source sand culture pot trial (Chapter 7) confirmed that nitrate-N uptake resulted in a decrease in anion uptake, including P, while ammonium-N uptake resulted in an increase in P uptake by the radiata pine seedlings.

In the field the addition of urea-N to soils will provide NH_4^+-N which is available for plant uptake or can be nitrified to NO_3^--N. The Taheke soils have a high potential for nitrification while at Ashley the potential is very low (data not presented). It is reasonable to presume that urea-N added to the Taheke site would be converted to NO_3^--N and, if this was the major form of N available for tree uptake, may have resulted in a decrease in P uptake even though the Bray 2 P soil levels suggest that P should not be a nutritional problem for radiata pine at this site.

Table 9.1: Comparison of nutrient levels in the upper horizons of the Taheke ex-pasture and Ashley Forest soils.

	Depth (cm) [@]	Taheke ex-pasture site	Depth (cm)	Ashley Forest
pH	0-25	5.5	0-10	5.1[#]
			10-20	5.1[#]
Organic C (%)	0-25	4.9	0-10	2.6
			10-20	2.1
Total N (%)	0-10	0.44 - 0.67	0-10	0.13
	10-20	0.26 - 0.42	10-20	0.13
Mineral N ($\mu g\ g^{-1}$)	0-10	73 - 171	0-10	40[#]
	10-20	17 - 60	10-20	35[#]
Bray 2 P (Ext.1, $\mu g\ g^{-1}$)	0-25	95	0-10	9.4
			10-20	4.8
Bray 2 K (me%)	0-25	0.50	0-10	0.26
			10-20	0.23
Bray 2 Ca (me%)	0-25	5.5	0-10	1.5[#]
			10-20	1.2[#]
Bray 2 Mg (me%)	0-25	0.88	0-10	1.4
			10-20	1.2

[@] The means at 0-25cm depth are from the two sampled profiles at the Taheke ex-pasture site (**Table 3.9a and 3.9b**). Data from the 0-10 and 10-20cm depths were the minimum and maximum values, at each depth, from the Taheke ex-pasture site trial plots in both August and February (**Table 3.6**)

[#] Data from the profiles sampled in the control plots (N_0B_0) at Ashley Forest. The other data are means for all of the sampled profiles at Ashley Forest.

The results from Ashley confirmed that P was a nutrient that may be limiting tree growth in this forest. While fertiliser P was added as a basal dressing at the start of the trial, foliar P concentrations 4 months later were still marginal to low and retranslocation appeared to be an important mechanism for supplying adequate P for new growth. This was particularly the case where N had been added.

In the sand culture pot trials (Chapter 8) it appeared that while increasing N addition could decrease plant P uptake, increasing P addition could increase plant N uptake. Radiata pine growing on ex-pasture sites have high concentrations of foliar N. The sand culture pot trial results suggest that N concentrations may be further increased if the amount of P available for radiata pine uptake is also high (**Table 8.21b**), while Cu uptake may be reduced (**Table 8.23b**) with a subsequent decrease in shoot Cu:N ratios (**Table 8.22**). Since a reduction in Cu:N ratios was associated with a greater number of stem kinks at the Taheke ex-pasture site, high amounts of P in an ex-pasture soil may indirectly increase the potential for stem deformity in radiata pine.

Magnesium was another nutrient that was affected by N addition at Taheke and Ashley. At Taheke the foliar Mg concentrations in February declined from marginal to low, with increasing N addition. At Ashley the effect of N was significant but the concentrations of Mg remained at satisfactory levels in March.

Bray 2 Mg was the only measured soil nutrient that was found in higher amounts at Ashley than Taheke (**Table 9.1**). The difference in the amount of Bray 2 Mg between the sites was not great but perhaps the uptake of Mg at Taheke may not have matched the rapid growth of the trees or there may have been competition with other cations, such as Ca^{2+} or K^{+}, at uptake. The amounts of Bray 2 Ca in the Taheke soil were 3 to 4 times higher than those at Ashley.

A major focus of this study was the effect of N addition on the micronutrient nutrition of radiata pine. At both Taheke and Ashley the effect of increasing additions of N on foliar micronutrient concentrations was generally not significant. In the soils, the amount of Cu associated with the most readily available plant fraction, SEO (soil solution/exchangeable/organic matter), was similar in the Rotorua and Ashley soils (**Figure 6.1**). foliar concentrations of Cu were marginal at Taheke and only slightly higher at Ashley. The amount of Zn in the SEO fraction was considerably higher in the Rotorua soils (**Figure 6.3**) and the foliar concentrations were approximately 38μg g^{-1} compared to 28μg g^{-1} at Ashley. Foliar B concentrations were marginal in February at Taheke and in the B_0 plots at Ashley in March. The soils at both sites had similar amounts of B associated with the non-specifically adsorbed and specifically adsorbed fractions (**Figure 6.5**) in the top 20cm of the profiles. These results suggest that the amount of micronutrients associated with the 'plant available' fractions may give a good indication of the micronutrient status of radiata pine. Also, while large quantities of macronutrients may be added to ex-pasture soils, micronutrients are generally not. Therefore, the amount of micronutrients in ex-pasture soils may become limiting.

At Ashley, the retranslocation of P and B may have been a significant process for its redistribution to new growth. Sampling the 2 year-old needles at Ashley, in November 1991, indicated that retranslocation of N, P, K, Cu and Zn had occurred since May 1990 in Block 1. These results suggest that, with time, more and more of the nutrients will be retranslocated within radiata pine at Ashley. This result could be expected for a nutritionally poor soil.

At Taheke the needle weights were not measured so the significance of retranslocation could not be calculated. As the foliar concentrations of P and Mg were low, the addition of N may have increased needle growth, resulting in their dilution and retranslocation. While the nutrient status of the soils at Taheke appeared high, this may not have reflected nutrient availability for tree uptake, particularly in competition with the pasture.

Another important effect of N addition is the increase in shoot:root ratio. In the sand culture pot trials there was a reduction in seedling root weight with increased N addition. The roots therefore absorbed more nutrient per unit weight and became more efficient. In the sand culture pot trials, the nutrient supply was maintained and, essentially, large seedlings with small root systems were not disadvantaged. In the field, however, root systems need to grow in order to explore the soil volume for nutrients. If the capacity of the radiata pine root systems in ex-pasture soils, such as Taheke, is small compared to the proportionally larger shoot, then the root system may not be able to maintain a constant supply of nutrients, particularly micronutrients and other nutrients in small amounts in the soil, to the shoot. This may also have occurred at Ashley where the biomass study indicated that there was an above-ground response to added N. As the root system was not completely sampled, the effect of N addition on root growth is unclear. If the shoot:root ratio increased, as results from

the sand culture pot trials suggest, then nutrient uptake, particularly of P and B, by the root system would have to increase to match tree demand or these nutrients may limit tree growth.

A further consideration at Taheke is the effect of nitrate-N on root morphology. In the N source pot trial, the root systems of the nitrate-fed seedlings were quite different, in colour and morphology, to that of the ammonium-fed seedlings. The nitrate-fed roots had significantly higher concentrations of K, Cu, B and particularly Ca, Mg and Fe (**Table 7.4b**). One or more of these nutrients may have been involved in the changes of the root system. As the nitrate seedlings still had adequate growth, it is difficult to ascertain whether the nitrate-fed root system was significantly affected by the changes.

While the addition of N had many effects on other nutrients, as well as N, the addition of B, at Ashley and in the sand culture pot trials described in Chapter 8, generally only affected changes in plant B. This may relate to the fact that B did not increase plant growth and therefore did not increase nutrient dilution or retranslocation. However, the addition did reduce the amount of retranslocation of B at Ashley. The fact that retranslocation of B occurred at Ashley confirmed the findings of Hill and Lambert (1981) and Hopmans and Clerehan (1991) - that B can be mobile within radiata pine and can therefore be retranslocated. At Ashley, a site with marginal B levels for radiata pine growth, the ability to retranslocate B may be important for supplying new growth with adequate concentrations of this micronutrient.

9.3 PHYSICAL GROWTH RESPONSE OF RADIATA PINE TO FERTILISER ADDITION

In general, increasing the addition of N affected radiata pine growth by increasing seedling height, fascicle weight, seedling shoot weight, seedling shoot:root ratios and the number of epicorms per seedling; and decreasing seedling root dry weight.

At Taheke and Ashley, increasing N addition did not significantly affect tree height or, at Taheke only, the amount stem deformity or DBH. As the generally recognised tree responses to the presence of high N levels in the soil are an increase in the weight of individual needles and the size of the tree canopy, the physical measurements taken at the Taheke ex-pasture site may not have been appropriate for radiata pine growth in this system. However, it appeared that the amount of N added to the Taheke ex-pasture site was relatively insignificant compared with the amount of N already present in the soil.

At Ashley, a site of poorer nutrient status than Taheke, a radiata pine growth response was expected. As with Taheke, the measurement of tree height may not have been appropriate especially as increasing N addition did increase fascicle weights and possibly the tree canopy. Even after 3 years there was no significant response in tree height or DBH to N and/or B addition at Ashley. However, the biomass study suggested that there had been a significant response, in terms of tree weight, to fertiliser addition. At Ashley there is also the question of other nutrients, particularly P, limiting tree growth despite the addition of basal P in the field trial.

During the Ashley field trial the addition of B did not significantly affect tree height or fascicle weight. However, when the radiata pine trees were later biomassed, it appeared that the addition of B a year earlier had significantly increased the weight of various age classes of needles and branches (Appendix 2a) both alone ($N_0B_{7.4}$) and with the addition of N ($N_{400}B_{7.4}$) compared to the control (N_0B_0).

While B addition at Ashley appeared to have a significant and positive effect on the growth of radiata pine, in the P_4 ammonium by B pot trial (Chapter 8) the increasing addition of B resulted in a decrease in the magnitude of a number of seedling growth variables. The reasons behind this negative B effect were unclear particularly as this B effect did not occur in the P_8 pot trial.

In the field, the precise measurement of radiata pine stem deformity was a difficult task because of the difficulty of access into the tree to measure the deformities, the obscured view of the centre leader when scoring from ground level, the three-dimensional nature of the stem deformity syndromes (which angle does one take?), and the subjectivity of using a scoring method. While Birk *et al.* (1989) have provided some detailed guidelines for the description of stem deformity in radiata pine, the question still remains as to how precise and detailed the description needs to be in order to correlate them with internal measurements of nutrient concentrations and ratios and other factors such as soil physical and chemical properties.

In this study, the measurements of stem deformity in radiata pine trees in the field were subjective and while an attempt was made to give the measurements a real value by describing the amount of deviation in terms of the size of stem diameter at that point, the results are only useful in investigating the deformities within the particular trial in which they were taken. It is important that a consistent system, such as that described by Birk *et al* (1989), is widely adopted and used so that comparisons between stem deformity and their possible cause on different sites can be made.

In the pot trial situation, where a lot of the practical difficulties associated with measuring stem deformity in the field no longer existed, there was still the question of the three dimensional nature of the stem growth. The measurement of 'height difference' was a simplistic method of describing the loss in straight vertical stem growth by any deviations to the side seen as kinking and horizontal growth. The results from this method were more conclusive than the field results in highlighting the role of N in the development of stem deformities, but the method is only of use when small pliable seedlings are being measured.

At Taheke there were significant correlations between site measurements of N and stem deformity. It appears that the response of trees to soil N may be dependent on factors such as the low amounts of other nutrients limiting tree growth, the availability of soil moisture and the role of pasture competition (see section 9.3.1). Also at Taheke, the correlation of stem deformity with soil N measurements changed depending on the season - August (winter) versus February (summer) - and the corresponding stage of tree growth. In August, high amounts of soil N correlated with less stem deformity while in February the amount of stem deformity increased with increasing amounts of soil N. Perhaps it is the amount of soil N, particularly mineral N, available for tree uptake when radiata pine growth flushes are occurring that is the critical factor in the relationship between soil N and the development of radiata pine stem deformity that appeared to exist at Taheke.

The pot trial studies with radiata pine confirmed that increasing N addition can have a significant effect on the level of stem deformity. However, unlike the literature which suggests that high levels of nitrate in the soil may cause stem deformities, these studies suggested that the amount of N available for uptake, rather than the form as nitrate or ammonium, may be the most important factor.

At Taheke, higher amounts of stem deformity in February were associated with higher N and Zn concentrations in the foliage while the number of kinks in the leader decreased as Cu:N ratios increased. While the Cu:N ratios were not significantly correlated with the amount of stem

deformity, it appears that low Cu:N ratios may indicate a tree's vulnerability to mechanical factors such as wind and rain which may deform the new soft growth of radiata pine.

In both of the ammonium by B pot trials (Chapter 8) neither Cu concentrations nor Cu:N ratios in the shoots were correlated with height difference. However, in these pot trials there was a common, and significant, correlation between B:N ratios in the shoots and height difference (**Figure 8.35c**). As B:N ratios increased the amount of height difference decreased.

Thus, the field and pot trials present two contrasting results. The Taheke trials indicated that an increase in Cu:N ratios may reduce the number of kinks in radiata pine trees growing in an ex-pasture agroforestry system. For radiata pine seedlings grown in a sand culture pot trial, an increase in B:N ratios was associated with straighter growth.

Both Cu and B have been previously implicated in the development of radiata pine stem deformities on ex-pasture sites. It is possible that the lack of either nutrient, given high levels of N and rapid radiata pine growth, may produce similar growth deformities as Cu is important in cell wall metabolism and B is reported to be important in lignification processes. A lack of either Cu or B or an imbalance between these micronutrients and N may result in softer new growth that could be deformed by mechanical factors, like wind, in conjunction with gravity. The occurrence of the syndrome may depend on the availability of these micronutrients in the soil and, perhaps more importantly, the ability of radiata pine root system to take up the micronutrients from the soil.

9.4 EFFECT OF SITE ON RADIATA PINE GROWTH AND NUTRITION

The chemical and physical features of a soil are affected by its land-use history. Previous land-use was an important factor which contributed to the higher amounts of total N% and Bray 2 P and Mg, and the greater nitrification potential of the soils at the Taheke agroforest compared to the soils of the plantation forest at Whakarewarewa. Other factors involved may have been the different types and depths of volcanic parent material.

The extent to which N addition affects radiata pine nutrition and growth depends on the growing system. From the Taheke study it appears that the addition of N fertilisers are unlikely to significantly affect radiata pine growth and nutrition if the system already contains large amounts of soil N. At a site such as Ashley, a response from radiata pine to the addition of N is much more likely.

Site factors such as soil water holding capacity, drainage patterns, exposure to wind, and soil variability in nutrient content may have been important and unmeasured influences on the growth and nutrition of radiata pine at both Taheke and Ashley. The field trial at Taheke indicated the importance of underlying site factors as was emphasised by the significance of the 'plot' effect for a number of measurements including greater tree height, stem deformity (see **Table 3.10**) and foliar N and P concentrations which were associated with higher amounts of total N% and Bray 2 P in the soil.

At Ashley, the effect of site factors was accounted for, to a certain extent, by blocking replicates of fertiliser treatments on areas of similar topography. The block effect at Ashley was significant for tree heights and stem deformity (**Figure 4.11**). The designation of blocks at the Ashley trial site was based on the visual landform which was assumed to reflect changes in soil properties. However, site

variability within these blocks and high coefficients of variation in some nutrient measurements may have reduced the significance of some of the fertiliser effects.

One of the common features of the Taheke and Ashley field trials was the presence of a competitive vegetation represented by the rank pasture at Taheke and a predominantly gorse and broom weed cover at Ashley. This competing vegetation would affect the availability of nutrients and water to the young radiata pine from the upper horizons of the soil profile and, in both trials, may have represented a major sink for the added fertilisers. Unfortunately the weed components of both systems were not measured but previous studies have highlighted the substantial effect that the presence and removal of competing vegetation can have on radiata pine tree growth (e.g. Clinton 1990).

The lack of response of the Taheke trial to N addition suggested that further study of high rates of N on the nutrition of radiata pine would be more conclusive on a soil of poorer nutrient status which was why Ashley Forest was chosen. However, while N addition did have an effect on radiata pine tree growth and nutrition, the presence of weeds and possibly their subsequent uptake of N (and other nutrients) from the soil may have reduced the potential tree response to added N and accounted for the fact that the addition of N did not have a significant effect on total N% in the soil. In contrast, B addition at Ashley was still evident in soil B measurements a year later. These results indicated that the added B remained in the soil for much longer than added N and was therefore available for further tree uptake. Added N, if taken up by the competing vegetation, would not have been lost from the system and may become available for tree uptake through normal nutrient cycling processes.

The climate appeared to be an important site factor at both Taheke and Ashley where there was evidence that the amount of rainfall influenced the concentrations of nutrients in radiata pine foliage. Although the correlations were based on a small number of measurements, the relationship between radiata pine foliar nutrient concentrations, and presumably nutrient uptake, and rainfall may be of importance in the foliar diagnosis of nutrient status at low rainfall sites such as Ashley. The Ashley correlations also indicated that B fertilisation increased foliar B concentrations and reduced the significance of rainfall on B concentrations.

9.5 GENETICS

Recent radiata pine research has highlighted the important role that tree genetics has in determining root growth, nutrient uptake, nutrient concentrations and a variety of other tree physiological and metabolic processes.

The genetics of radiata pine was not studied here and its effects in the uptake of nutrients and its role in the development of stem deformity was unquantified. Using a large number of trees per plot (i.e. 10 at Taheke and Ashley) and five seedlings per pot in the pot trials was an attempt to minimise the effects of radiata pine genetic variation.

At Taheke, not all trees exhibited stem deformity symptoms. The straight growing trees were able to grow normally in an environment that could cause stem deformities in others - what was their genetic advantage and was there an interaction with various site factors?

In Australia, radiata pine trees have been selected to grow with a straight form on ex-pasture sites. Thus the problems encountered with poor tree form on pasture sites has been solved but the question still remains as to what genetic traits allow radiata pine to grow in soils of high N content without developing stem deformities.

9.6 SUMMARY

During this study, the addition of N had many effects on radiata pine growth and nutrition in a variety of growing systems.

At the Taheke ex-pasture site, N addition increased the foliar concentrations of N but it also resulted in a decrease in the concentrations of other nutrients such as P, Ca and Mg. The processes by which nutrient concentrations and amounts in the foliage declined were dilution and retranslocation of the nutrient probably in response to an increase in plant growth as a result of N fertiliser addition. This occurred for P and B in the fascicle study at Ashley Forest. This study highlighted the potential mobility of B which was retranslocated from fascicles during periods of low rainfall. This was related to the B supply to the tree as its retranslocation was reduced where B fertilisers had been supplied.

It appeared that N balances with Cu and B were related to radiata pine growth deformities. At the Taheke ex-pasture site, a decrease in Cu:N ratios in the foliage was associated with an increase in the number of kinks in the upper stem of the trees. In the N by B pot trials, a decrease in B:N ratios in the seedling shoots was associated with an increase in the seedling height difference - a simple measure of stem deformity. An increase in the rate of N addition resulted in a decrease in B:N ratios in the N by B pot trial and Cu:N ratios in February at the Taheke ex-pasture site.

The form of N supplied for seedling uptake (ammonium or nitrate) was shown to affect radiata pine growth and nutrition in a sand culture pot trial. Depending on the rate of N addition, seedlings had significantly higher shoot and root weights when ammonium-fed. When nitrate was the form of N added, there was an increase in the uptake of Ca, Mg and Fe while the uptake of P was reduced. The root systems of the nitrate-fed seedlings were both darker in colour and more finely and numerously branched than ammonium-fed roots. There was also a build up of Cu, B and Fe in the nitrate-fed roots compared with their concentrations in the shoots. This indicated that some mechanism may have been preventing micronutrient transport to the shoots. Previous workers have suggested that organic acids, produced during NRA within the roots, may bind micronutrients and prevent their movement.

The major effect of increasing rates of added B on radiata pine was an increase in B concentrations and amounts within the plant as occurred in the Ashley Forest fascicle and biomass studies and the N by B pot trials. However, the results from the biomass study at Ashley Forest suggested that the addition of B at 7.4kg ha^{-1} significantly increased tree growth at this site.

At both the Ashley Forest site and the Taheke ex-pasture site, there was no evidence of residual fertiliser N in the soil. At Ashley Forest, B addition significantly increased the non-specifically adsorbed and specifically adsorbed B fractions in the top 20cm of the soil profile. At both sites the competing vegetation may have been an important sink for the added fertilisers.

A comparison of soils from Whakarewarewa Forest at the Taheke ex-pasture site indicated that previous landuse history can have a large affect on the nutrient status of the soils.

9.7 FURTHER RESEARCH

The growth and nutrition of radiata pine in ex-pasture sites, and the sharing of site resources with the pasture component, involves a wide variety of opportunities for research in many different disciplines. For radiata pine, a species that has been extensively researched in plantation systems, ex-pasture sites present a new challenge being met by genetic selection and different techniques for the diagnosis of its nutritional state.

Many unquantified factors that may have affected radiata pine tree nutrition and growth have been identified in this study. The following describes some of the areas in which further research could be carried out.

❖ Genetic selection has provided radiata pine trees that do not develop severe stem deformities when grown in ex-pasture systems. However, it is still not known what tree characteristics have been selected for that allow the trees to maintain a straight stem during vigorous growth in the presence of high N availability.

❖ The form of N available for uptake can have significant effects on the growth of radiata pine seedlings and the morphology of the root system. It is not known what changes occur in the root system that alter the colour and branching characteristics as a result of nitrate nutrition. There is also the question of reduced micronutrient transport to the shoot of nitrate-fed seedlings and whether the micronutrients are being bound in organic acids produced during NRA. If these changes occur in a sand culture pot trial, do they also occur for radiata pine growing in ex-pasture systems where nitrate may be the predominant form of N available for tree uptake?

❖ It appears that micronutrient balances with N in the foliage are an indication of the susceptibility of radiata pine to develop stem deformities in systems where N availability for uptake is high. It is unclear whether the changing relationship between N and micronutrients, such as Cu and B, is indirect, via dilution, or a result of some other mechanism within the plant.

❖ In ex-pasture systems, the soil levels of P can be high. At high levels of available P in the sand culture pot trial, the uptake of N by radiata pine was increased. This may also occur in ex-pasture systems. P may also affect the uptake and utilisation of other nutrients, particularly Cu.

❖ Ex-pasture systems with radiata pine as a component are complex when considering the competition for and availability of nutrients and water and the cycling of nutrients through the tree and pasture components. Although there has been work in this area with nutrients such as N and P, little is known about the dynamics of micronutrients in this system.

❖ Rainfall, and subsequent soil moisture levels, control many aspects of nutrient availability in the soil and the uptake of nutrients by plants. While there appears to be a relationship between rainfall and foliar B concentrations (and probably other nutrients) in low rainfall areas, to date this information has not been used to improve either the diagnosis of radiata pine's nutrient status from foliar analysis or subsequent fertiliser recommendations.

❖ In ex-pasture systems, the nitrification pathway is important in supplying N for plant uptake. The microbial population mediating this pathway may change during a radiata pine rotation in an ex-pasture system. If so, what factors cause this change and how does the form and amount of N available for tree uptake change through the rotation?

❖ Standard foliar values for assessing the nutrient status of radiata pine are currently based on nutrient concentrations. However, the use of nutrient:N ratios appear to be useful in diagnosing possible nutrient imbalances in radiata pine growing in ex-pasture systems.

❖ It may be possible to develop a measure of 'plant available' fractions of micronutrients such as B in the soil that give an indication of the micronutrient status of a site for radiata pine growth.

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Appendix 1a: Effect of N and/or B fertiliser additions on a) macronutrient and b) micronutrient concentrations in radiata pine foliage from December 1989 to May 1990 at Ashley Forest. For each nutrient concentration at each sampling date, means followed by the same letter were not significantly different ($p<.05$).

a)		N_0 B_0	N_0 $B_{3.7}$	N_0 $B_{7.4}$	N_{200} B_0	N_{200} $B_{3.7}$	N_{200} $B_{7.4}$	N_{400} B_0	N_{400} $B_{3.7}$	N_{400} $B_{7.4}$
N%	Dec	1.59 bc	1.56 c	1.57 c	1.73 a	1.74 a	1.68 ab	1.70 a	1.74 a	1.75 a
	Jan	1.58 b	1.59 b	1.67 ab	1.69 ab	1.76 a	1.72 ab	1.80 a	1.72 ab	1.80 a
	Mar	1.63 de	1.65 cde	1.58 e	1.76 abcd	1.70 bcde	1.70 bcde	1.85 a	1.83 ab	1.78 abc
	May	1.62 c	1.61 c	1.60 c	1.72 bc	1.70 bc	1.68 bc	1.91 a	1.80 ab	1.81 ab
P%	Dec	0.189 a	0.193 a	0.194 a	0.187 a	0.189 a	0.178 a	0.175 a	0.172 a	0.191 a
	Jan	0.176 a	0.163 abc	0.171 ab	0.164 abc	0.144 cd	0.154 abcd	0.135 d	0.140 cd	0.146 bcd
	Mar	0.120 a	0.123 a	0.118 a	0.087 bc	0.084 bc	0.098 b	0.074 c	0.074 c	0.089 bc
	May	0.118 a	0.114 a	0.112 ab	0.085 cd	0.096 bc	0.086 cd	0.075 d	0.075 d	0.078 d
K%	Dec	1.09 abc	1.13 a	1.03 bc	1.05 abc	1.10 ab	1.05 abc	1.05 abc	1.00 c	1.07 abc
	Jan	1.01 a	1.04 a	1.04 a	0.97 ab	0.97 ab	0.95 ab	0.81 b	0.88 ab	0.97 ab
	Mar	0.86 abc	0.97 a	0.93 ab	0.73 cd	0.80 d	0.80 bcd	0.82 bcd	0.73 cd	0.74 cd
	May	0.83 a	0.85 a	0.82 a	0.78 a	0.78 a	0.75 a	0.74 a	0.76 a	0.66 a
Ca%	Dec	0.21 ab	0.20 b	0.22 ab	0.22 ab	0.23 a	0.21 ab	0.21 ab	0.22 ab	0.22 ab
	Jan	0.32 a	0.31 a	0.31 a	0.26 b	0.32 a	0.31 a	0.31 a	0.32 a	0.32 a
	Mar	0.42 ab	0.40 ab	0.43 a	0.40 b	0.42 ab	0.40 ab	0.40 b	0.40 ab	0.41 ab
	May	0.49 a	0.47 abc	0.47 ab	0.44 c	0.47 ab	0.46 abc	0.44 c	0.44 c	0.45 bc
Mg%	Dec	0.131 abc	0.126 bc	0.131 abc	0.132 abc	0.141 a	0.130 abc	0.122 c	0.134 abc	0.135 ab
	Jan	0.114 a	0.114 a	0.117 a	0.103 ab	0.113 ab	0.110 ab	0.099 b	0.107 ab	0.111 ab
	Mar	0.126 a	0.119 ab	0.128 a	0.107 b	0.120 ab	0.114 ab	0.104 b	0.110 ab	0.113 ab
	May	0.128 a	0.111 abc	0.123 ab	0.104 bc	0.117 abc	0.112 abc	0.100 c	0.107 bc	0.102 c

Appendix 1a: (continued).

µg g^{-1}		N_0 B_0	N_0 $B_{3.7}$	N_0 $B_{7.4}$	N_{200} B_0	N_{200} $B_{3.7}$	N_{200} $B_{7.4}$	N_{400} B_0	N_{400} $B_{3.7}$	N_{400} $B_{7.4}$
Cu	Dec	4.5 a	4.7 a	4.5 a	4.7 a	4.9 a	5.1 a	4.7 a	4.6 a	4.9 a
	Jan	4.6 a	4.7 a	4.4 a	4.6 a	5.0 a	5.0 a	4.5 a	4.6 a	4.5 a
	Mar	5.0 a	4.8 ab	4.6 ab	4.5 b	5.0 ab	5.0 ab	4.9 ab	4.9 ab	4.8 ab
	May	4.5 ab	4.1 b	4.2 ab	4.5 ab	4.5 ab	4.7 a	4.2 ab	4.6 ab	4.3 ab
Zn	Dec	26 a	27 a	27 a	27 a	28 a	25 a	26 a	25 a	27 a
	Jan	27 ab	27 ab	28 ab	27 ab	30 a	27 ab	26 ab	24 b	28 ab
	Mar	30 a	29 a	29 a	28 a	28 a	28 a	27 a	26 a	27 a
	May	32 a	31 ab	29 ab	30 ab	29 ab	29 ab	28 ab	26 b	28 ab
B	Dec	10.7 b	13.4 ab	15.4 a	12.0 b	12.0 b	15.3 a	11.8 b	12.0 b	13.5 ab
	Jan	32 bcd	31 cd	36 abc	29 d	32 bc	37 ab	28 d	32 bcd	39 a
	Mar	11.3 cd	17.6 b	24.4 a	9.4 d	14.9 bc	24.5 a	9.1 d	12.3 cd	18.4 b
	May	12.8 de	20.7 bc	29.7 a	10.3 e	17.8 bcd	30.3 a	9.9 e	14.9 cde	22.9 b

Appendix 1b: Effect of N and/or B fertiliser addition on weight of radiata pine fascicles from December 1989 to May 1990 at Ashley Forest. For each sampling date, means followed by the same letter were not significantly different ($p<.05$).

mg fascicle^{-1}	N_0 B_0	N_0 $B_{3.7}$	N_0 $B_{7.4}$	N_{200} B_0	N_{200} $B_{3.7}$	N_{200} $B_{7.4}$	N_{400} B_0	N_{400} $B_{3.7}$	N_{400} $B_{7.4}$
Dec	31 abcd	29 cd	32 abc	33 ab	36 a	29 cd	27 d	30 bcd	32 abcd
Jan	57 abc	47 c	56 abc	64 a	61 ab	60 ab	50 bc	64 a	54 abc
Mar	76 ab	65 b	72 ab	81 a	82 a	75 ab	72 ab	79 a	79 a
May	89 ab	78 b	86 ab	94 a	96 a	92 ab	89 ab	90 ab	93 ab

Appendix 1c: Effect of N and/or B fertiliser addition on the amount of a) macronutrient and b) micronutrient per radiata pine fascicle with sampling date from December 1989 to May 1990 at Ashley Forest. For each nutrient at each sampling date, means followed by the same letter were not significantly different ($p<.05$).

mg fascicle^{-1}		N_0 B_0	N_0 $B_{3.7}$	N_0 $B_{7.4}$	N_{200} B_0	N_{200} $B_{3.7}$	N_{200} $B_{7.4}$	N_{400} B_0	N_{400} $B_{3.7}$	N_{400} $B_{7.4}$
N	Dec	0.50 bcd	0.45 d	0.50 bcd	0.58 ab	0.62 a	0.49 cd	0.46 d	0.52 bcd	0.55 abc
	Jan	0.90 ab	0.75 b	0.92 ab	1.09 a	1.07 a	1.04 a	0.91 ab	1.10 a	0.97 ab
	Mar	1.24 abc	1.08 c	1.14 bc	1.42 a	1.39 a	1.27 abc	1.34 ab	1.44 a	1.40 a
	May	1.43 abc	1.25 c	1.37 bc	1.62 ab	1.63 ab	1.56 ab	1.70 a	1.61 ab	1.68 a
P	Dec	0.059 abc	0.056 bcd	0.062 ab	0.063 a	0.066 a	0.052 cd	0.048 d	0.052 cd	0.060 cd
	Jan	0.099 ab	0.078 cd	0.095 abc	0.103 a	0.087 abcd	0.091 abc	0.069 d	0.089 abcd	0.079 abcd
	Mar	0.092 a	0.080 ab	0.085 ab	0.070 bcd	0.069 bcd	0.073 abc	0.054 d	0.058 cd	0.070 bcd
	May	0.108 a	0.089 abc	0.096 ab	0.081 bc	0.092 ab	0.079 bc	0.067 c	0.067 c	0.073 bc
K	Dec	0.34 abc	0.33 bc	0.33 abc	0.35 ab	0.39 a	0.31 bc	0.29 c	0.30 bc	0.34 abc
	Jan	0.58 a	0.49 ab	0.58 a	0.62 a	0.59 a	0.58 a	0.41 b	0.56 ab	0.52 ab
	Mar	0.68 a	0.63 a	0.67 a	0.59 a	0.57 a	0.60 a	0.58 a	0.57 a	0.57 a
	May	0.77 a	0.66 a	0.70 a	0.69 a	0.75 a	0.71 a	0.65 a	0.69 a	0.64 a
Ca	Dec	0.066 bcde	0.059 de	0.070 bc	0.074 ab	0.082 a	0.061 cde	0.056 e	0.067 bcd	0.069 bcd
	Jan	0.183 abc	0.144 c	0.177 abc	0.175 abc	0.194 ab	0.193 ab	0.151 bc	0.202 a	0.168 abc
	Mar	0.32 ab	0.26 c	0.31 abc	0.32 ab	0.34 a	0.30 abc	0.29 bc	0.32 ab	0.32 ab
	May	0.43 ab	0.37 b	0.41 ab	0.41 ab	0.46 a	0.43 ab	0.39 ab	0.40 ab	0.42 ab
Mg	Dec	0.040 bcd	0.037 de	0.042 bc	0.044 b	0.050 a	0.038 cde	0.033 e	0.040 bcd	0.042 bc
	Jan	0.063 ab	0.054 bc	0.065 ab	0.065 ab	0.068 a	0.065 ab	0.050 c	0.068 a	0.060 abc
	Mar	0.092 a	0.078 b	0.091 a	0.085 ab	0.097 a	0.085 ab	0.075 b	0.087 ab	0.087 ab
	May	0.108 ab	0.087 d	0.105 ab	0.096 bcd	0.112 a	0.102 abc	0.088 cd	0.095 bcd	0.094 bcd

Appendix 1c: (continued)

µg fascicle $^{-1}$		N_0 B_0	N_0 $B_{3.7}$	N_0 $B_{7.4}$	N_{200} B_0	N_{200} $B_{3.7}$	N_{200} $B_{7.4}$	N_{400} B_0	N_{400} $B_{3.7}$	N_{400} $B_{7.4}$
Cu	Dec	0.139 bc	0.137 bc	0.144 bc	0.158 ab	0.172 a	0.147 abc	0.129 c	0.139 bc	0.153 abc
	Jan	0.26 abc	0.23 c	0.25 abc	0.30 abc	0.30 b	0.31 a	0.23 bc	0.30 abc	0.25 abc
	Mar	0.38 ab	0.31 c	0.33 bc	0.36 abc	0.41 a	0.38 abc	0.36 abc	0.39 ab	0.38 ab
	May	0.40 ab	0.32 b	0.36 ab	0.43 a	0.43 a	0.43 a	0.37 ab	0.42 a	0.40 a
Zn	Dec	0.79 bc	0.78 bc	0.86 abc	0.91 ab	1.01 a	0.73 bc	0.70 c	0.75 bc	0.87 abc
	Jan	1.50 ab	1.29 b	1.52 ab	1.69 a	1.83 a	1.61 ab	1.31 b	1.54 ab	1.50 ab
	Mar	2.2 ab	1.9 b	2.0 ab	2.3 a	2.3 a	2.1 ab	2.0 ab	2.0 ab	2.1 ab
	May	2.7 a	2.4 a	2.5 a	2.8 a	2.7 a	2.6 a	2.5 a	2.3 a	2.6 a
B	Dec	0.34 bc	0.39 abc	0.50 a	0.41 abc	0.43 abc	0.44 ab	0.32 c	0.36 bc	0.42 abc
	Jan	1.81 ab	1.46 b	1.96 a	1.79 ab	1.96 a	2.19 a	1.42 b	2.03 a	2.10 a
	Mar	0.90 cde	1.14 bcd	1.77 a	0.77 de	1.21 bc	1.82 a	0.66 e	0.98 cd	1.49 ab
	May	1.17 de	1.61 cd	2.59 ab	0.99 e	1.70 cd	2.78 a	0.88 e	1.33 de	2.17 bc

Appendix 2: Effect of N and B fertilisers on the dry weight and nutrient content of the biomassed components of radiata pine one year after fertiliser addition at Ashley Forest. Total amounts for the above-ground tree are also presented at the bottom of each table. For each component, means with the same letter were not significantly different ($p<.05$). The distribution of data from components marked with an "*" was skewed and no further statistics were carried out on the means.

a) Component dry weight

Component	N_0B_0	$N_0B_{7.4}$	$N_{400}B_0$	$N_{400}B_{7.4}$	CV%
Current Needles	217 b	429 a	211 b	355 ab	31.4
1 Year Needles	360 d	642 c	855 b	1018 a	9.9
2 Year Needles	43 b	179 a	86 b	82 b	45.5
3 Year Needles	18 c	68 a	26 bc	50 ab	38.8
4 Year Needles	1.6 a	7.5 a	2.6 a	8.8 a	82.9
Current Branch	108 b	233 ab	155 ab	276 a	40.2
1 Year Branch	153 b	385 ab	327 ab	563 a	39.7
2 Year Branch	53 b	224 a	96 b	95 b	55.5
3 Year Branch	20 b	77 a	30 b	59 ab	45.8
4 Year Branch	8.7 ab	20.8 a	3.2 b	13.0 ab	76.6
Current Stem	19.2 ab	21.6 a	7.6 b	14.4 ab	45.2
1 Year Stem	79 b	147 ab	248 a	162 ab	49.4
2 Year Stem	102 b	254 ab	339 a	219 ab	30.8
3 Year Stem*	107	451	197	244	74.9
4 Year Stem	213 a	363 a	255 a	372 a	33.4
1 Year Bark	13 a	24 a	49 a	36 a	62.6
2 Year Bark	17 b	34 b	65 a	48 ab	45.6
3 Year Bark	16 a	58 a	42 a	44 a	78.1
4 Year Bark	34 a	58 a	50 a	69 a	44.1
Total (g $tree^{-1}$)	1,583	3,676	3,044	3,728	

b) Component N content (g)

Component	N_0B_0	$N_0B_{7.4}$	$N_{400}B_0$	$N_{400}B_{7.4}$	CV%
Current Needles	4.18 b	7.22 a	4.17 a	6.41 ab	27.9
1 Year Needles	5.9 c	8.9 b	14.3 b	15.2 a	12.2
2 Year Needles	0.55 b	1.99 a	1.19 ab	1.02 ab	48.0
3 Year Needles	0.23 c	0.72 a	0.310 bc	0.62 ab	38.4
4 Year Needles	0.016 a	0.061 a	0.032 a	0.094 a	89.5
Current Branch	1.15 b	2.01 ab	1.83 ab	2.88 a	34.7
1 Year Branch	0.78 b	1.80 ab	1.91 ab	2.62 a	38.7
2 Year Branch	0.19 b	0.64 a	0.29 ab	0.39 ab	51.8
3 Year Branch	0.054 a	0.155 a	0.085 a	0.167 a	55.4
4 Year Branch	0.021 a	0.039 a	0.011 a	0.034 a	78.5
Current Stem	0.189 a	0.163 a	0.089 a	0.132 a	27.9
1 Year Stem	0.18 a	0.23 a	0.44 a	0.33 a	49.2
2 Year Stem	0.20 b	0.39 ab	0.50 a	0.32 ab	34.9
3 Year Stem[a]	0.17	0.52	0.27	0.36	74.3
4 Year Stem[a]	0.33	0.45	0.33	0.58	37.9
1 Year Bark[a]	0.10	0.16	0.41	0.26	68.2
2 Year Bark	0.11 b	0.19 b	0.48 a	0.34 ab	48.3
3 Year Bark	0.10 a	0.32 a	0.29 a	0.30 a	81.4
4 Year Bark	0.19 a	0.26 a	0.32 a	0.45 a	45.9
Total N (g $tree^{-1}$)	14.6	26.2	27.2	32.5	

c) Component P content (g)

Component	N_0B_0	$N_0B_{7.4}$	$N_{400}B_0$	$N_{400}B_{7.4}$	CV%
Current Needles	0.67 b	1.29 a	0.47 b	0.68 b	29.3
1 Year Needles	0.61 b	1.08 ab	1.49 a	1.58 a	27.1
2 Year Needles	0.053 b	0.272 a	0.096 b	0.086 b	44.6
3 Year Needles	0.026 b	0.094 a	0.030 b	0.080 a	40.8
4 Year Needles	0.0044 a	0.0106 a	0.0029 a	0.0100 a	65.5
Current Branch	0.20 b	0.47 a	0.22 b	0.36 ab	29.9
1 Year Branch	0.15 b	0.34 ab	0.26 ab	0.47 a	39.5
2 Year Branch[a]	0.032 b	0.134 a	0.043 b	0.047 b	64.6
3 Year Branch	0.019 a	0.038 a	0.029 a	0.025 a	46.9
4 Year Branch	0.0038 a	0.0081 a	0.0046 a	0.0052 a	68.6
Current Stem	0.032 ab	0.047 a	0.011 c	0.019 bc	32.6
1 Year Stem	0.049 a	0.089 a	0.087 a	0.078 a	31.8
2 Year Stem	0.058 b	0.097 ab	0.136 a	0.089 ab	31.4
3 Year Stem	0.034 b	0.152 a	0.067 ab	0.049 ab	76.8
4 Year Stem[a]	0.083	0.153	0.120	0.133	30.8
1 Year Bark[a]	0.015	0.029	0.053	0.050	73.4
2 Year Bark	0.021 b	0.036 b	0.071 a	0.042 b	32.9
3 Year Bark	0.020 a	0.062 a	0.043 a	0.047 a	73.1
4 Year Bark	0.036 b	0.064 ab	0.046 ab	0.110 a	55.9
Total P (g $tree^{-1}$)	2.12	4.47	3.28	3.96	

d) Component K content (g)

Component	N_0B_0	$N_0B_{7.4}$	$N_{400}B_0$	$N_{400}B_{7.4}$	CV%
Current Needles	2.56 b	4.76 a	2.25 b	3.66 ab	30.1
1 Year Needles	2.40 b	5.01 ab	4.18 ab	6.90 a	33.7
2 Year Needles	0.32 b	1.35 a	0.37 b	0.56 b	57.3
3 Year Needles	0.096 b	0.485 a	0.092 b	0.260 ab	57.1
4 Year Needles	0.006 a	0.042 a	0.006 a	0.062 a	133.8
Current Branch	1.52 b	3.03 a	1.70 ab	2.71 ab	32.5
1 Year Branch	0.87 b	2.31 ab	1.85 ab	2.55 a	43.4
2 Year Branch*	0.18	0.77	0.26	0.31	66.5
3 Year Branch	0.045 b	0.140 a	0.044 b	0.104 ab	51.4
4 Year Branch	0.0141 a	0.0276 a	0.0071 a	0.0209 a	80.2
Current Stem	0.189 ab	0.282 a	0.074 b	0.124 b	44.1
1 Year Stem	0.25 a	0.41 a	0.42 a	0.33 a	32.7
2 Year Stem	0.23 a	0.39 a	0.44 a	0.27 a	42.9
3 Year Stem*	0.19	0.54	0.21	0.23	76.3
4 Year Stem	0.34 a	0.44 a	0.24 a	0.38 a	43.6
1 Year Bark	0.067 a	0.108 a	0.158 a	0.136 a	48.0
2 Year Bark	0.066 b	0.122 b	0.203 a	0.101 b	29.2
3 Year Bark*	0.055	0.209	0.102	0.088	66.6
4 Year Bark	0.108 a	0.188 a	0.147 a	0.150 a	46.7
Total K (g $tree^{-1}$)	9.5	20.6	12.8	19.0	

e) Component Ca content (g)

Component	N_0B_0	$N_0B_{7.4}$	$N_{400}B_0$	$N_{400}B_{7.4}$	CV%
Current Needles	0.43 b	1.02 a	0.52 b	0.74 ab	37.0
1 Year Needles	1.4 b	2.7 a	2.9 a	3.7 a	21.7
2 Year Needles	0.19 b	0.88 a	0.53 ab	0.38 b	48.1
3 Year Needles	0.11 c	0.48 a	0.18 bc	0.36 ab	34.7
4 Year Needles	0.013 a	0.067 a	0.017 a	0.076 a	82.8
Current Branch	0.11 b	0.27 ab	0.23 ab	0.39 a	34.4
1 Year Branch	0.23 b	0.68 ab	0.62 b	1.16 a	37.7
2 Year Branch	0.09 b	0.42 a	0.20 b	0.26 ab	45.2
3 Year Branch	0.033 c	0.143 a	0.057 bc	0.123 ab	43.7
4 Year Branch	0.014 a	0.044 a	0.009 a	0.027 a	85.3
Current Stem	0.017 a	0.019 a	0.006 a	0.020 a	83.6
1 Year Stem[a]	0.044	0.071	0.150	0.107	58.8
2 Year Stem	0.06 b	0.14 a	0.20 a	0.15 a	30.4
3 Year Stem[a]	0.066	0.269	0.109	0.183	72.7
4 Year Stem	0.13 b	0.22 ab	0.15 b	0.27 a	28.8
1 Year Bark	0.021 b	0.037 ab	0.073 a	0.078 a	45.8
2 Year Bark	0.029 b	0.063 ab	0.125 a	0.098 a	41.6
3 Year Bark	0.030 a	0.114 a	0.073 a	0.098 a	70.9
4 Year Bark	0.061 b	0.115 ab	0.119 ab	0.171 a	38.8
Total Ca (g $tree^{-1}$)	3.08	7.75	6.27	8.39	

f) Component Mg content (g)

Component	N_0B_0	$N_0B_{7.4}$	$N_{400}B_0$	$N_{400}B_{7.4}$	CV%
Current Needles	0.36 a	0.66 a	0.36 a	0.47 a	38.0
1 Year Needles	0.63 b	0.99 ab	1.33 a	1.35 a	18.1
2 Year Needles	0.074 b	0.277 a	0.162 b	0.108 b	39.1
3 Year Needles	0.035 b	0.127 a	0.057 b	0.084 ab	39.4
4 Year Needles	0.0037 a	0.0149 a	0.0050 a	0.0186 a	117.5
Current Branch	0.15 a	0.25 a	0.20 a	0.30 a	44.4
1 Year Branch	0.23 b	0.47 ab	0.48 ab	0.66 a	37.6
2 Year Branch	0.083 b	0.245 a	0.126 ab	0.128 ab	49.6
3 Year Branch	0.026 b	0.067 a	0.029 b	0.059 ab	42.7
4 Year Branch	0.0091 a	0.0194 a	0.0051 a	0.0134 a	85.5
Current Stem	0.0239 a	0.0204 ab	0.0075 b	0.0126 ab	43.0
1 Year Stem	0.048 a	0.064 a	0.107 a	0.083 a	42.1
2 Year Stem	0.055 b	0.097 ab	0.142 a	0.091 ab	35.8
3 Year Stem[a]	0.053	0.153	0.066	0.105	71.9
4 Year Stem	0.100 a	0.127 a	0.087 a	0.153 a	30.5
1 Year Bark[a]	0.016	0.022	0.044	0.034	53.3
2 Year Bark	0.021 b	0.030 b	0.071 a	0.045 ab	42.2
3 Year Bark	0.021 a	0.047 a	0.038 a	0.044 a	64.1
4 Year Bark	0.044 a	0.051 a	0.053 a	0.066 a	36.4
Total Mg (g $tree^{-1}$)	1.98	3.73	3.37	4.42	

g) Component Cu content (mg)

Component	N_0B_0	$N_0B_{7.4}$	$N_{400}B_0$	$N_{400}B_{7.4}$	CV%
Current Needles	1.3 a	2.3 a	1.6 a	2.0 a	29.4
1 Year Needles	1.8 b	2.7 b	4.4 a	4.1 a	21.3
2 Year Needles	0.12 b	0.47 a	0.30 ab	0.22 ab	53.6
3 Year Needles	0.073 b	0.189 a	0.084 b	0.177 a	31.5
4 Year Needles	0.006 a	0.022 a	0.011 a	0.027 a	87.5
Current Branch	0.66 a	1.17 a	1.13 a	1.70 a	48.5
1 Year Branch	0.72 b	1.77 ab	1.65 ab	2.41 a	39.3
2 Year Branch	0.17 b	0.63 a	0.34 ab	0.34 ab	48.1
3 Year Branch	0.058 b	0.230 a	0.096 ab	0.167 ab	53.4
4 Year Branch	0.022 ab	0.048 a	0.010 b	0.34 ab	72.2
Current Stem	0.123 ab	0.130 a	0.063 b	0.075 ab	35.5
1 Year Stem	0.312 b	0.459 ab	0.690 a	0.501 ab	33.1
2 Year Stem	0.32 b	0.55 ab	0.85 a	0.45 b	35.4
3 Year Stem[a]	0.34	0.92	0.43	0.51	56.7
4 Year Stem	0.59 a	0.76 a	0.63 a	0.75 a	32.7
1 Year Bark	0.051 a	0.101 a	0.221 a	0.196 a	68.0
2 Year Bark	0.059 b	0.104 ab	0.297 a	0.223 ab	71.1
3 Year Bark	0.056 a	0.208 a	0.190 a	0.169 a	92.4
4 Year Bark	0.161 a	0.177 a	0.197 a	0.241 a	53.7
Total Cu (mg $tree^{-1}$)	6.9	12.9	13.2	14.6	

h) Component Zn content (mg)

Component	N_0B_0	$N_0B_{7.4}$	$N_{400}B_0$	$N_{400}B_{7.4}$	CV%
Current Needles	6.5 a	12.3 a	7.0 a	9.4 a	39.2
1 Year Needles	11 b	21 a	24 a	23 a	22.9
2 Year Needles	1.4 b	6.5 a	3.3 b	2.2 b	44.8
3 Year Needles	0.57 b	3.53 a	0.98 b	2.19 a	44.3
4 Year Needles	0.09 a	0.42 a	0.10 a	0.55 a	122.2
Current Branch	3.1 b	5.7 ab	4.2 ab	7.1 a	38.6
1 Year Branch	4.4 b	10.2 ab	10.0 ab	13.3 a	47.2
2 Year Branch	1.9 b	4.9 a	2.8 ab	2.9 ab	43.3
3 Year Branch	0.61 b	1.64 a	0.67 b	1.63 a	38.6
4 Year Branch	0.22 a	0.22 a	0.09 a	0.29 a	80.1
Current Stem	0.36 a	0.37 a	0.17 b	0.22 ab	31.1
1 Year Stem	1.04 b	1.40 ab	2.48 a	1.80 ab	38.4
2 Year Stem	1.3 a	2.5 a	3.9 a	2.1 a	46.3
3 Year Stem[s]	1.4	3.5	1.7	2.3	68.7
4 Year Stem	2.2 a	2.9 a	2.5 a	3.5 a	35.9
1 Year Bark	0.38 b	0.54 ab	1.13 a	0.90 ab	47.4
2 Year Bark	0.55 b	0.82 b	2.07 a	1.37 ab	41.6
3 Year Bark	0.61 a	1.48 a	1.11 a	1.27 a	68.1
4 Year Bark	1.22 a	1.34 a	1.31 a	1.89 a	42.4
Total Zn (mg $tree^{-1}$)	38.9	81.3	69.5	77.9	

i) Component B content (mg)

Component	N_0B_0	$N_0B_{7.4}$	$N_{400}B_0$	$N_{400}B_{7.4}$	CV%
Current Needles	2.4 b	9.9 a	2.2 b	7.7 a	37.5
1 Year Needles	3.0 d	20.1 b	7.3 c	27.8 a	14.7
2 Year Needles[s]	0.50	6.01	0.76	1.98	61.8
3 Year Needles	0.19 b	2.24 a	0.26 b	1.08 b	53.5
4 Year Needles	0.016 b	0.249 a	0.028 b	0.212 a	76.5
Current Branch	1.3 b	3.6 ab	1.7 b	4.1 a	47.4
1 Year Branch	1.6 b	5.3 ab	3.4 b	7.3 a	45.2
2 Year Branch[s]	0.53	2.30	0.79	1.22	60.4
3 Year Branch	0.16 b	0.63 a	0.23 ab	0.54 ab	54.8
4 Year Branch	0.066 ab	0.154 a	0.025 b	0.099 ab	66.0
Current Stem	0.23 ab	0.37 a	0.09 b	0.22 ab	44.5
1 Year Stem	0.31 b	0.70 ab	0.88 a	0.78 ab	43.5
2 Year Stem	0.46 b	1.34 a	1.25 a	0.98 ab	39.1
3 Year Stem[s]	0.39	1.48	0.57	0.97	79.2
4 Year Stem	0.79 a	1.39 a	0.89 a	1.57 a	37.4
1 Year Bark	0.21 b	0.62 ab	0.66 ab	0.78 a	44.4
2 Year Bark	0.26 b	0.83 ab	0.93 a	1.05 a	44.4
3 Year Bark[s]	0.28	1.55	0.59	1.01	79.2
4 Year Bark	0.62 a	1.61 a	0.74 a	1.60 a	46.5
Total B (mg $tree^{-1}$)	13.3	60.4	23.3	61.0	